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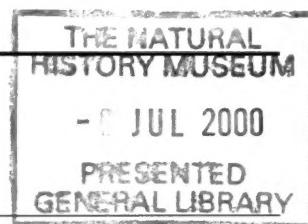
# A new species of *Heisteria* (Olacaceae) from Mesoamerica

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**SYNOPSIS.** A new species of Olacaceae from Mesoamerica, *Heisteria povedae*, is described and illustrated. Its range of variation is described and relationships to other Mesoamerican members of the genus briefly discussed.

While preparing treatments of the family Olacaceae for *Flora Mesoamericana* and the *Manual de plantas de Costa Rica*, it became clear that the widespread species treated as *Heisteria macrophylla* Oerst. in Sleumer's (1984) *Flora Neotropica* account of the family included at least two elements. The type of *H. macrophylla* comes from the area along the Río San Juan near the Costa Rica/Nicaragua border, and material from the lowland Atlantic slope forests matches the type quite well (see below). The majority of specimens identified as *H. macrophylla* are significantly different from the type, and despite being the most widespread component of *H. macrophylla* sensu Sleumer, do not have a name. We therefore coin a new name for this widespread, common species here.

***Heisteria povedae* Q. Jiménez & S. Knapp, sp. nov.** Type: Costa Rica, Guanacaste, Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 8 February 1995, A. Azofeifa 25 (INB!-holotype; BM!, CR!, F!, MO!-isotypes).

Fig. 1.

Frutices vel arbores parvae; ramuli valde alati albo-punctati vel striati, alis in caulis maturioribus persistenibus; folia in statu sicco viridi-olivacea punctulata; fructus niger globosi nitidi leviter porcati; calyx fructifer patente ruber margine sinuatus; pedunculi fructiferi crassi.

**Shrubs or small trees**, 1–5 m; bark pale. **Branchlets** strongly angular, markedly flattened and strongly 2-winged, occasionally 4-winged, the wings persisting to older stems, pale olive green, often white striped. **Leaves** 6–20 × 2.5–6.5 cm, elliptic to narrowly elliptic, shape very variable even within a single collection, usually drying a very pale olive green, strongly pellucid dotted below, matte on both surfaces; venation drying bright pale yellow or white, all orders clearly visible; apex acuminate, occasionally acute; margins revolute, slightly undulate, paler; base acute to cuneate; petioles 0.5–1.1 cm, rugose and pale green along entire length. **Inflorescence** a few-flowered glomerule of 5–7 flowers; bracts glabrous, pale green; pedicels 1–2 mm. **Flowers** white, the buds ellipsoid; calyx cupuliform, the lobes c. 0.25–0.5 mm, either mere teeth from the calyx rim or more or less equalling the tube; petals c. 2 mm, glabrous within; filaments 1–1.5 mm, liguliform to petaloid. **Fruit** 7–9 × 7–10 mm, often wider than long, globose, strongly ridged and somewhat shiny, black; fruiting calyx 1.9–2.5 cm, unlobed, the margins sinuate, spreading or slightly cupping the base of the fruit, fleshy, red; peduncles 5–9 mm, very thick.

**COMMON NAMES.** Guatemala, Quezaltenango: 'arito de montaña'

(Standley 68338), 'palo de bastón' (Steyermark 33360); El Salvador, Ahuachapan: 'ojos de pava' (Sandoval & Chinchilla 281).

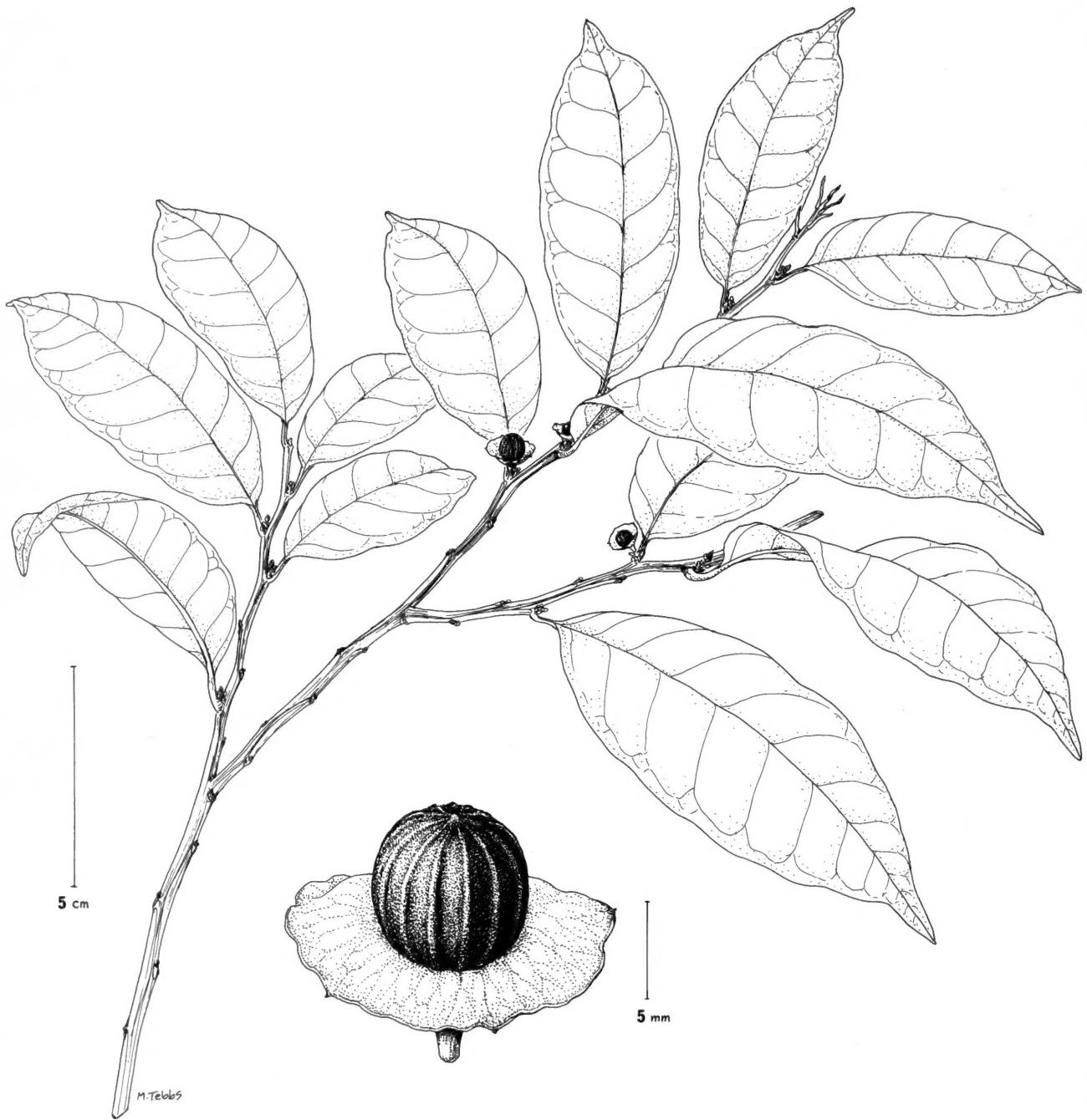
**ETYMOLOGY.** This species is dedicated to the Costa Rican botanist Luis Jorge Poveda, in recognition of his great knowledge of Costa Rican plants, and in honour of his many contributions to the knowledge and conservation of plants in Mesoamerica.

**DISTRIBUTION.** *Heisteria povedae* is endemic to Mesoamerica, occurring from Chiapas to Panama. It is generally found at middle elevations, (200)–800–1500(–2000) m, in lowland forest, premontane forest and occasionally in the oak forests of the Cordillera de Talamanca in Costa Rica. *Heisteria povedae* is more common on the Pacific slope, but some have been collected on the Atlantic slope. (Fig. 2).

#### SPECIMENS EXAMINED.

**MEXICO. Chiapas:** Palomeque, Mt. Ovando, 1400 m, 16 February 1969, Hernández M., R. 528 (MO, NY); Volcán Tacana, Unión, 1400 m, 17–23 March 1939, Matuda, E. 2787 (MEXU); La Grada, Escuintla, 12 August 1947, Matuda, E. 16807 (F); Cacalut, Escuintla, 15 August 1947, Matuda, E. 16875 (F); Corcega, Pueblo Nuevo Com., 15 April 1948, Matuda, E. 17658 (F); Las Nubes, Mt. Ovando, 1150 m, 15 November 1949, Matuda, E. 18756 (F, MEXU); Arroyo de la Cuchilla, arriba de Finca Prusia (SW de Jaltenango), 1500 m, 22 February 1951, Miranda, F. 6965 (US); Mun. Acayocagua, Mt. Ovando, trail to c. 5 km above Finca La Magnolia, 3 km N. of Los Cacao and 13 km N. of Acayocagua on road to Olondrina, 1200–1500 m, 29 May 1985, Thomas, W. & Villaseñor, J.L. 3663 (MEXU, NY); near Rancho de Finca Prusia, Mun. Angel Albino Corzo, 2400 ft, 23 January 1968, Ton, Alush Shilom 3566 (F, MEXU, MO); along the Río Cuztepeques near Finca Cuztepeques, 2400 ft, 26 March 1968, Ton, Alush Shilom 3865 (F, MEXU, MO); Monte Ovando, 1950 m, 9 January 1987, Vázquez T., M. 3899 (NY).

**GUATEMALA. Chimaltenango:** lower and middle SW slopes of Volcán Fuego, above Finca Montevideo, along Barranco Espinazo and tributary of Río Pantaleón, 1200–1600 m, 20 September 1942, Steyermark, J.A. 52087 (F, NY). **Escuintla:** Finca Monterrey, S. slope of Volcán de Fuego, 1140–1260 m, 5 February 1939, Standley, P.C. 64570 (F). **Quezaltenango:** Finca Pireneos, below Santa María de Jesus, 1350–1380 m, 11 March 1939, Standley, P.C. 68199, 68338, 68396 (F); along old road between Finca Pireneos & Patzulin, 200–1400 m, 9 February 1941, Standley, P.C. 86950, 86959, 86992 (F); along Quebrada San Gerónimo, Finca Pireneos, lower S-facing slopes of Volcán Santa María, between Santa María de Jesus & Calahuaché, 1300–2000 m, 1–2 January 1940, Steyermark, J.A. 33360 (F, NY); off Hwy. 95, c. 4 miles S. of Santa María de Jesus, W. side of Volcán Sta. María, 29 June 1973, Stone, D.E. 3492 (F, MEXU, MO, NY); Finca St. John of Mr Whitehead, c. 5 km S. of Santa María de Jesus, SE slopes of Volcán Santa María, 4300–5500 ft, 17 May 1966, Walker, J.W. 443 (F, NY, US). **San Marcos:** La Trinidad c. 2 km from Finca Armenia above San Rafael,

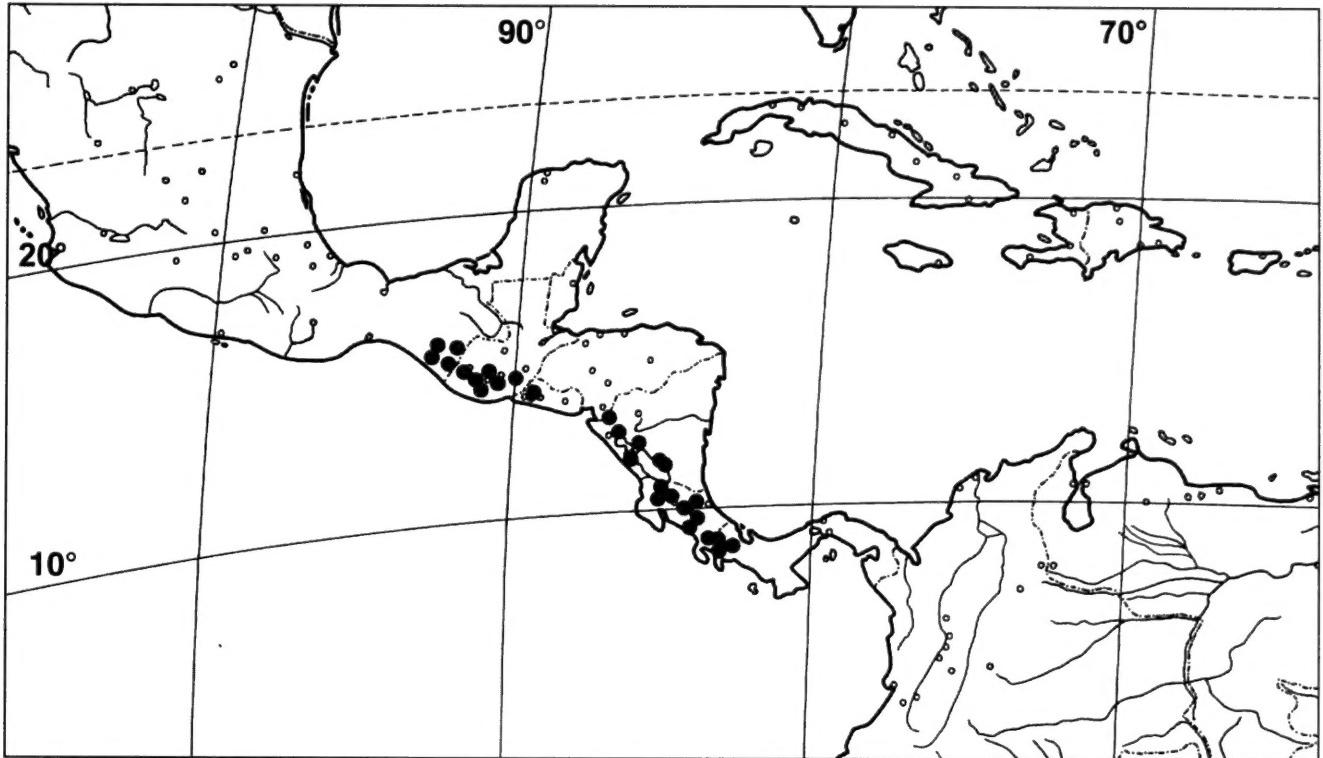


**Fig. 1** *Heisteria povedae* (habit based on INBio 149 (MO) & Fuentes et al. 67 (MO); fruit based on Davidse et al. 28398 (MO)).

1100–1250 m, 12 July 1977, Croat, T.B. 40873 (MO); above Finca El Porvenir on Todos Santos Chiquitos, lower S.-facing slopes of Volcán Tajamulco, 1300–1500 m, 7 March 1940, Steyermark, J.A. 37080 (F). **Sololá:** cercanías de Patulul, 240 m, December 1929, García Salas, J. 1418 (F); S.-facing slopes of Volcán Atitlán, above Finca Moca, 1000–1250 m, 20 June 1942, Steyermark, J.A. 47903 (F). **Suchitepéquez:** SW lower slopes of Volcán Zunil, between Finca Montecristo & Finca Asturias, SE of Santa María de Jesús, 1200–1300 m, 1 February 1940, Steyermark, J.A. 35281 (F); Finca Moca, 3000–4400 ft, 10 January 1935, Skutch, A.F. 2109 (BM, F, NY, US). **Zacatepéquez:** Acatepeque, 4300 ft, March 1892, Donnell-Smith, J. 2479 (US); Volcán de Agua, 9000 ft, November 1889, Heyde & Lux (JDS) 4446 (MO, NY).

**EL SALVADOR. Ahuachapán:** Mun. San Fco. Menéndez, Hacienda San Benito, al N. de Campana (El Imposible), 13°49'N, 89°56'W, 23 February 1982, Sandoval & Chinchilla 281 (MO (B, LAGU)); Sierra de Apaneca, in region of Finca Colima, 17–19 January 1922, Standley, P.C. 20185 (F, MO, US).

**NICARAGUA. Boaco:** Cerro Mombachito, 4 km NE de Camoapa, 700–1000 m, 1 February 1979, Grijalva, A. & Araquistan, M. 60 (MEXU, MO); Monte Azul, San José de los Remates, 1000–1200 m, 12°38'N, 85°43'W, 12 February 1983, Moreno, P.P. 20309 (MO); NE de Mombachito, 11 May 1982, Sandino, J.C. 2829 (MO); upper SW slope of Cerro Mombachito, S. of road between Boaco and Camoapa, 900–1000 m, c. 12°24'N, 85°33'W, 3 October 1979, Stevens, W.D. et al. 14589 (MEXU, MO, NY); upper W. slope of Cerro



**Fig. 2** Distribution of *Heisteria povedae*.

Mombachito, 900–1000 m, c. 12°24'N, 85°33'W, 8 October 1979, Stevens, W.D. et al. 14776 (MO). **Chontales:** Cerro Oluma, c. 3 km SW de Ciudad Cuapa, 700–740 m, 12°18'N, 85°20'W, 3 January 1984, Grijalva, A. et al. 3370 (MO, NY); Cerro Las Nubes, El Tamagás y Loma San Gregorio, c. 2 km al N. de Santo Domingo, 600 m, 20 January 1984, Grijalva, A. & Ríos, D. 3471 (MO); 4 km NW of Cuapa, ridgetops and summits of Cerro Oluma, 700–775 m, 12°18'N, 85°23'30" W, 23 September 1983, Nee, M. 28445 (MO); Cerro Buenavista, 5 km N. of Cuapa, 15 July 1976, Neill, D.A. 634 (MO). **Matagalpa:** Santa María de Ostuma, Cordillera Central de Nicaragua, 1200–1500 m, 1960–1961, Heller, A.H. 61 (F); camino al Cerro La Carlota, a 2 km de la carretera al Tuma, 1040–1100 m, 12°58'N, 85°52'W, 5 March 1982, Moreno, P.P. 15656, 15699 (MO); Cerro Matapalo, 9 km de Matagalpa cerretera a El Tuma, 1000–1100 m, 12°57'N, 85°51'W, 23 February 1983, Moreno, P.P. & Robleto, W. 20485 (MO, NY); El Trebol, 7 km al S. de Peñas Blancas, carretera a El Tuma, 800–900 m, 13°12'N, 85°39'W, 23 February 1983, Moreno, P.P. & Robleto, W. 20535 (MO); 6–10 km NE of Matagalpa, road to El Tuma, 1000 m, 14–16 January 1963, Williams, L.O. et al. 23840 (F, NY, US). **Zelaya:** Cerro La Pimienta number 1, summit and area adjacent, 900–980 m, c. 13°45'N, 84°59'W, 13 April 1979, Pipoly, J.J. 5108 (MO); c. 6.3 km S. of bridge at Colonia Yolania and c. 0.8 km S. of ridge of Serranías de Yolania on road to Colonia Manantiales (Colonia Somoza), 200–300 m, c. 11°36–37'N, 84°22'W, 29–31 October 1977, Stevens, W.D. 4865 (NY); S. slope of Cerro El Inocente, 1000–1050 m, c. 13°46'N, 85°00'W, 8 March 1978, Stevens, W.D. 6741 (MEXU, MO, NY).

**COSTA RICA. Alajuela:** Monteverde, Peñas Blancas river valley, 800 m, 10°20'N, 84°43'W, 28 February 1990, Bello, E. 1959 (INB); colinas de San Pedro de San Ramón, 1075–1300 m, 29 October 1925, Brenes, A.M. 4574 (CR, F); Piedades au San Pedro de San Ramón, 1100 m, 26 October 1925, Brenes, A.M. 4559 (F); San Pedro et a Piedades, San Pedro de San Ramón, 1075 m, 22 June 1926, Brenes, A.M. 4881 (CR, F); La Palma de San Pedro de San Ramón, 1075–1100 m, 24 September 1926, Brenes, A.M. 4977 (F); La Palma de San Pedro de San Ramón, 1050–1100 m, 7 December 1926, Brenes, A.M. 5187 (F); La Palma de San Pedro de San Ramón, 1050 m, 17 July 1927, Brenes, A.M. 5606 (CR, F); entre Guachipelín y Volcán de la Vieja, 26 May 1932, Brenes, A.M. 15524 (CR); Río Jesus y el Picacho del Mondongo,

Santiago de San Pedro de San Ramón, 1 January 1937, Brenes, A.M. 21847 (F, NY); E. of Río San Rafael and S. of hot springs, W. of La Marina, 500 m, 10°23'N, 84°23'W, 19 May 1968, Burger, W.C. & Stolze, R.G. 5025 (F, NY); San Rafael de San Ramón, 24 February 1945, Echeverría C., J.A. 4128 (CR, F); Reserva Forestal de San Ramón, 870–1120 m, 10°13'15"N, 84°36'00"W, 29 April 1993, Flores, K. 98 (INB); Finca Buen Amigo, San Luis Monteverde, 1100 m, 10°16'20"N, 84°49'30"W, 29 June 1993, Fuentes, Z. 393 (INB); Cerro Chato, 23 April 1990, Funk, V.A. et al. 10825 (CR); Río Chiquito, c. 40 km road to Upala, 800 m, October 1982, Gómez, L.D. 18614 (BM, MO); slopes of Miravalles, above Bijagua, c. 1500 m, November 1982, Gómez, L.D. et al. 19180 (MO); Alto Santiago de San Ramón, 1200 m, 27 September 1980, Gómez-Laurito, J. 5888 (CR); Río San Lorencito, límite E. de la Reserva Forestal San Ramón, 800–900 m, 23 February 1984, Gómez-Laurito, J. 9923 (CR, F); Reserva Forestal San Ramon, 900–1200 m, 10°13'N, 84°37'W, 12–15 March 1987, Gómez-Laurito, J. 11394 (F); Monteverde, Peñas Blancas river valley, 800 m, 10°20'N, 84°43'W, 7 October 1986, Haber, W. & Cruz, E. 5672 (CR); Reserva Forestal San Ramón, río San Lorencito, 850–1100 m, 10°18'N, 84°34'W, 30 May–1 June 1986, Hammel, B. et al. 15293 (CR, MO); Bijagua, El Pilón, cabeceras del Río Celeste, 700 m, 10°49'N, 84°27'W, 16 November 1987, Herrera, G. 297 (US); Finca La Constancia, Buena Vista, San Carlos, 850 m, 3 March 1963, Jiménez, A. 423 (CR, F, NY); San Ramón, N. of town towards Los Angeles, 1150 m, 27 January 1964, Lems, K. 01-4 (NY); near Río San Rafael, 2 km W. of La Marina, llanura de San Carlos, 550 m, 17 February 1966, Molina R., A. et al. 17339 (BM, F, MO); Estación San Ramón, Parque Nacional Guanacaste, 550 m, 10°52'55"N, 85°24'05"W, 27 January 1995, Quesada, F. 186 (INB); 5 km N. de Lago Arenal, c. Lago Cote, sendero Ilusión, 800–1000 m, 10°35'20"N, 84°55'50"W, 14 October 1994, Sánchez, J. 356 (CR); Reserva Forestal de San Ramón, 870–1120 m, 10°13'15"N, 84°36'00"W, 1 March 1992, Schmidt, E. 83 (INB); Alfaro Ruiz, Guadalupe de Zarcerio, 1625 m, 30 May 1938, Smith, A. H692 (MO, NY); Alfaro Ruiz, Guadalupe de Zarcerio, 1625 m, 30 May 1938, Smith, A. NY692 (NY); San Carlos, Villa Quesada, 850 m, 31 March 1939, Smith, A. 1880 (F, MO, NY); San Pedro, San Ramón, 1300 m, April 1913, Tonduz, A. 17656 (BM, CR, US); 2 km from Bijagua on road to San Miguel, along road from Cañas to Upala, 470 m, 7 November 1975, Utley

& Utley 3218 (F). **Cartago:** vicinity of Pejivalle, 600–850 m, January 1940, Skutch, A.F. 4581 (F, MO, NY, US). **Guanacaste:** Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 2 June 1990, Acevedo, D. 5, Alvarado, C. 15 (CR); Tilarán, March 1942, Acosta, M.A. 14 (CR); Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 23 September 1994, Alverson, W. & Christy, C.M. 2769 (CR); Área de Conservación Guanacaste, biological station on W. flank of Volcán Cacao, 1100 m, c. 10°55'32"N, 85°28'02"W, 23 July 1994, Alverson, W.S. & Flores, T.S. 3105 (CR, MO); Abangares, la Sierra y Río Cañas, 1000 m, 10°22'00"N, 84°55'00"W, Bello, E. 4959 (INB); E. slopes of Volcán Miravalles (Cerro la Giganta), above town of Río Naranjo, c. 800 m, 10°42'N, 85°07'W, 8 April 1973, Burger, W.C. & Gentry, J.L. 9143 (F); Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 29 October 1989, Chacón, I. 2520 (CR); Parque Nacional Guanacaste, Estación Cacao, Liberia, 1100 m, 10°55'45"N, 85°28'15"W, 18 November 1990, Chávez, C. 341 (MO); Estación Maritza, Parque Nacional Guanacaste, 600 m, 10°57'40"N, 85°29'40"W, 29 August 1990, Carballo, G. 215 (CR); Estación Maritza, Parque Nacional Guanacaste, 600 m, 10°57'40"N, 85°29'40"W, 29 August 1990, Chavarría, U. 178 (CR); Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 8 February 1995, Chinchilla 33 (INB); Parque Nacional Rincón de la Vieja, SE slopes of Volcán Santa María, above Estación Hacienda Santa María, 900–1200 m, 10°47'N, 85°18'W, 27–28 January 1983, Davidse, G. et al. 13369 (CR, MO); Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 9 February 1995, Gamboa, B. 51 (INB); Parque Nacional Rincón de la Vieja, Liberia, Cordillera Guanacaste, Estación Las Pailas, sendero Río Blanco, 1200 m, 10°47'50"N, 85°21'10"W, 5 November 1992, Garia, D. 32 (MO); Rincón de la Vieja National Park, Puesto Santa María, path to Mirador, c. 800 m, 27 January 1983, Garwood, N. et al. 717 (BM, F, MO, NY); ridges to N. of Río Las Flores, c. 1 km E. of Río Tenorio, hacienda Montezuma, 475–500 m, 10°40.5'N, 85°04.5'W, 24 January 1985, Grayum, M. & Herrera, G. 4854 (CR, MEXU); S. & E. slopes of ridge SE of Quebrada Zopilote, lower SE slope of Volcán Santa María, 850–940 m, 10°46.5'N, 85°18'W, 25 January 1986, Grayum, M. et al. 6243 (CR, NY); Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 12 July 1996, González, J. 1101 (INB); Parque Nacional Guanacaste, estación Maritza, sendero a la cima de Volcán Orosí, 600 m, 10°57.6'N, 85°29.6'W, 2 July 1989, IIINBio 142 (MO); Parque Nacional Guanacaste, Estación Maritza, sendero a la cima del Volcán Cacao, 600 m, 10°57.6'N, 85°29.6'W, 3 July 1989, IIINBio 119 (MO); Parque Nacional Rincón de la Vieja, 900–1200 m, 8 May 1972, Janzen, D.H. 401 (CR); El Silencio, Tilarán, 850 m, Jiménez, A. s.n. (F); Monteverde, 1450 m, 7 February 1966, Kern, P.M. 801 (NY); Santa Elena-Tilarán road, c. 2 km from Santa Elena, c. 1300 m, 17 February 1984, Khan, R. et al. 1096 (BM, MO); Estación Cacao, Parque Nacional Guanacaste, 1100 m, 10°55'32"N, 85°28'02"W, 30 May–1 June 1990, Maas, P.J.M. 18 (CR); Volcán Tenorio, 1200 m, 8 January 1993, Quirós, M. 1076a (CR); Estación Maritza, Parque Nacional Guanacaste, 600 m, 10°57'40"N, 85°29'40"W, 18 August 1993, Ramírez, R. 53 (INB); Parque Nacional Rincón de la Vieja, sendero de la Toma de Agua, a 3 km de la Estación, 1000 m, 10°46'05"N, 85°17'40"W, 17 September 1990, Rivera, G. 628 (MO); Parque Nacional Rincón de la Vieja, Estación Biológica Santa María, track to Agua Fria, 780 m, 10°46'N, 85°17'W, 19 June 1996, Short, M.J. & Stafford, P.J. 151 (BM, CR, INB); Parque Nacional Guanacaste, Volcán Cacao, 1000 m, 30 July 1987, Smith, J.F. & Frost, E. 425 (CR, F); Estación Maritza, Parque Nacional Guanacaste, 600 m, 10°57'40"N, 85°29'40"W, 31 August 1990, Solomon, J. 19111 (INB); El Silencio, near Tilarán, c. 750 m, 13 January 1926, Standley, P.C. & Valerio, J. 44596, 44602 (US); Quebrada Serena, SE of Tilarán, c. 700 m, 27 January 1926, Standley, P.C. & Valerio, J. 46178, 46196 (US); Naranjos Agrios, 600–700 m, 29 January 1926, Standley, P.C. & Valerio, J. 46495 (US); 3 km N. of Río Naranjo, near Continental Divide, 500 m, 10°52'N, 85°04'W, 5 January 1975, Taylor, J. 18103 (F); Tilarán, 20 July 1920, Valerio, J. 18 (US). **Limón:** 7 km SW of Bri bri, 100–250 m, 4 May 1983, Gómez, L.D. et al. 20430 (MO); vicinity of Guapiles, 300–500 m, 12–13 March 1924, Standley, P.C. 37331 (F, US); 6 miles inland from mouth of Estrella River, 19 April 1952, Stork, H.E. 4613 (NY). **Puntarenas:** Cerro Pando, ridges above Río Coto n and Río Negro, 1000–1800 m, 8°55'N, 82°45'W, 19–21 February 1982, Barringer, K. & Gómez, L.D. 1619 (F); Finca Las Cruces, San Vito de Java, c. 1300 m, 23 May 1971, Burch, D. 4616 (F); just E. of Monteverde on Pacific watershed, 1300–1450 m, 10°18'N, 84°48'W, 29 October–2 November 1975, Burger, W.C. & Baker, R. 9599, 9619 (F, MO); c. 2 km SE of Monteverde, on Pacific

watershed, 1400 m, 10°18'N, 84°48'W, 18–21 March 1973, Burger, W.C. & Gentry, J.L. 8765 (F); E. of Las Cruces and 5–6 km S. of San Vito, property of Mr Robert Wilson, 1100–1200 m, 8°47'N, 82°58'W, 15–16 January 1967, Burger, W.C. & Matta U., G. 4464 (BM, F, MO); E. of Quepos, Pacific slope of Talamancas, 150–250 m, 9°29'N, 84°03'W, 19 February 1977, Burger, W.C. et al. 10607 (F); just E. of Monteverde on Pacific watershed, 1300–1450 m, 10°18'N, 84°48'W, 24 February 1977, Burger, W.C. et al. 10706, 10847 (F, MO, NY); foothills of Cordillera de Talamanca, vicinity of Helechales, along Río Guineal, 1100–1200 m, 9°04'30"N, 83°05'W, 29 March 1984, Davidse, G. & Herrera Ch., G. 26242 (F); Cordillera de Talamanca, area around Río Canasta, 9.5 airlines miles NW of Aguas Caliente, between Cerro Frantzius & Cerro Pittier, 1500–1600 m, 9°02'N, 82°59'W, 6 September 1984, Davidse, G. et al. 28398 (MO); Monteverde, comunidad, 1400–1500 m, 28 November 1976, Dryer, V. 1004 (MO), 7 February 1977, Dryer, V. 1167 (F); San Luis, Monteverde, 1100 m, 10°16'33"N, 84°47'45"W, 17 December 1992, Fuentes, Z. et al. 67 (INB, MO); Monteverde, lower montane forest, 1400 m, 14 July 1990, Gentry, A. et al. 71672 (MO); La Tigra, Las Mellizas, 1280 m, August 1983, Gómez, L.D. et al. 21971 (BM, MO); San Luis, Monteverde, 1100 m, 10°16'33"N, 84°47'45"W, 10 September 1994, González, J. 400 (INB); Monteverde, 1300–1450 m, 10°18'N, 84°48'W, 10 June 1985, Grayum, M. & Hammel, B. 5389 (CR); Monteverde, lower community, 1350–1400 m, 25 February 1985, Haber, W.A. 1376 (MO), 29 August 1985, Haber, W. et al. 2532 (CR), 18 December 1988, Haber, W. 8905 (INB), 20 October 1990, Haber, W. 10089 (INB); Monteverde, lower community, 1350 m, 10°20'N, 84°50'W, 20 January 1986, Haber, W.A. & Wolf, J.A. 4284 (MEXU, MO); near Cerro Chivo, S. of Coton River, 1600–1800 m, 17 July 1983, Hazlett, D.L. 5240 (F); road from Pensión Flor March to Monteverde Cloud Forest Reserve, 1400–1500 m, 10°18'N, 84°48'W, 8 January 1987, Hill, S.R. et al. 17686 (NY); just E. of Monteverde on Pacific watershed, 1300–1450 m, 10°18'N, 84°48'W, 21 July 1977, Lawton, R.O. 1201 (F); Monteverde Cloud Forest Reserve, Hoge's Wood, 1320 m, 18 July 1979, Kopur, S. 155 (MO). **San José:** Cantón de Acosta, Zona Protectora Cerros de Escazú, cuenca del Río Tabarcia, falda W. de Cerro Cedral, por sendero a Londres, 1600–1700 m, 9°50'52"N, 84°04'40"W, 14 May 1994, Morales, J.F. 2758 (MO).

**PANAMA.** **Coclé:** foot of Cerro Pilón, above valle de Anton, 2000 ft, 28 March 1969, Porter, D.M. et al. 4676 (MO). **Colón:** 26 km from Transisthmica Highway on Santa Rita Ridge, NW facing slopes, 500 m, 9°26'N, 79°57'W, 21 October 1981, Knapp, S. et al. 1711 (MO). **Chiriquí:** trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, 1500–2000 m, 16 January 1939, Allen, P.H. 1589 (F, MO); Ojo de Agua, property of Ratibor Hartmann, vicinity of Santa Clara (between Volcán & Río Sereno), 1520 m, 8°51'N, 82°45'W, 17 June 1987, Croat, T.B. 66286 (US); road from Volcán to Río Serano, 16 km from Río Sereno, 29 June 1977, Folsom, J.P. 4048 (MO x2); Hartman finca, near Cerro Pando, c. 2000–2200 m, 8°52'N, 82°45'W, 22 August 1982, Hamilton, C. et al. 816 (MO x2); near Costa Rican border, 13 km by road S. of Río Sereno, Finca Hartmann, 1400–1500 m, 8°50'N, 82°45'W, 14 May 1991, Hensold, N. & McPherson, G. 1050 (MO, US); lower slopes of Cerro Pelota, 1800–2000 m, 8°53'N, 82°43'W, 10 October 1981, Knapp, S. 1481 (MO); forests and edges of cafetales of Finca Ojo de Agua, 1300 m, 8°51'N, 82°46'W, 14 October 1981, Knapp, S. 1578 (MO); Santa Clara region, 27 km NW of El Hato del Volcán, on coffee finca of Ratibor Hartmann called Ojo de Agua, 5000–5300 ft, 18 July 1975, Mori, S. & Bolten, A. 7215 (MO). **Panama:** along trail to top of Cerro Campana, 13 October 1974, Mori, S. & Kallunki, J. 2463 (MO); Cerro Campana, c. 10 km SW of Capira, on trail to summit, 870–1000 m, 7 December 1974, Mori, S. & Kallunki, J. 3565 (MO). **Veraguas:** vicinity of Escuela Agricultura Alto Piedra, near Santa Fe along trail to top of Cerro Tute, 2800–3200 ft, 3 April 1980, Antonio, T. 4003 (MO); 0.6 mile beyond Escuela Agrícola Alto Piedra, 730 m, 4 April 1976, Croat, T.B. & Folsom, J.P. 34069 (NY); above Santa Fe beyond Escuela Agrícola Alto Piedra, 1.8 miles beyond fork in road on Pacific slope, side of Cerro Tute, 5 April 1976, Croat, T.B. 34199 (MO); Cerro Tute, W. of Santa Fe, beyond Alto de Piedra, 600–800 m, c. 8°30'N, 81°07'W, 18 October 1985, McPherson, G. 7188 (MEXU); NW of Santa Fe, 1 km from Escuela Agrícola Alto de Piedra, slopes of Cerro Tute, 24 February 1975, Mori, S. & Kallunki, J. 4778 (MO, NY); along steep trail to summit of Cerro Tute c. 3 km above Escuela Agrícola Alto Piedra near Santa Fe, 2800–3200 ft, 4 January 1981, Systma, K. & Antonio, T. 3033 (MO).

Specimens here described as *Heisteria povedae* were called *H. acuminata* (Humb. & Bonpl.) Engl. by Burger (1983). He recognized

them as different to *H. macrophylla* Oerst. (s.s.), differentiating them by habitat: with plants of *H. macrophylla* s.s. growing in wet lowland forests and those of *H. acuminata* (sensu Burger) growing in drier more upland formations. Sleumer (1984) lumped these two taxa, stating however 'Specimens with leaves smaller than usual occur in Panama exclusively on its Pacific side'. The past decades of collecting, particularly in Costa Rica, have produced abundant specimens showing these two entities as distinct. *Heisteria povedae* is generally (as recognized by Burger) a plant of higher elevation, somewhat drier forests, than *H. macrophylla* s.s., which appears to be confined to the lowland rainforests on the Atlantic slope near the Costa Rica/Nicaragua border. The leaves of *H. povedae* are usually (but not always) smaller than those of *H. macrophylla* s.s., and dry a pale olive green with prominent yellowish venation. The stems of *H. povedae* are strongly flattened and winged at the tips, with the wings persisting onto quite large branchlets, and are markedly white punctulate or striate. Stems of *H. macrophylla* s.s. can be slightly winged when very small, but the angles rarely persist beyond the first two leaves.

Specimens from Limón province in Costa Rica are found within the distribution range of *Heisteria macrophylla* s.s. and may represent hybrids with that species. They have the typical yellowish venation, winged stems and subglobose fruit of *H. povedae*, but the leaves are generally larger than those from Pacific slope specimens. Future collecting and work on plants in the field will help to clarify the status of these populations.

*Heisteria acuminata*, the other widespread species of *Heisteria* in Mesoamerica, especially in Panama, differs from *H. povedae* in its ellipsoid fruit, and longer, thinner fruiting pedicels. The leaves of *H. acuminata* generally dry a darker greenish brown than those of *H. povedae*, and the branchlets are not markedly winged. *Heisteria acuminata* occurs in lowland forests from the Osa peninsula in Costa Rica to northern South America, and has been known in Mesoamerica as *H. longipes* Standl. or *H. cyanocarpa* Poepp. Material of *H. acuminata* from Popayán in southern Colombia may not match material from Mesoamerica (Jørgensen, pers. comm.), and the correct name for the material currently known as *H. acuminata* in Mesoamerica may change in future.

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# Three new species of *Pilea* (Urticaceae) from Costa Rica and Panama

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**SYNOPSIS.** Three new species of *Pilea* from Mesoamerica are described and illustrated: *P. conjugalis* A.K. Monro from Costa Rica and Panama which most closely resembles *P. pittieri* Killip, *P. adamsiana* A.K. Monro from Panama which most closely resembles *P. pallida* Killip, and *P. trichomanophylla* A.K. Monro, also from Panama, which is unique within the genus in having pinnately lobed isomorphic leaves. The affinities of these species are discussed and their position within Weddell's subdivisions of the genus indicated.

## INTRODUCTION

*Pilea* is the largest genus within the Urticaceae and one of the larger genera in the Urticales. It is distributed throughout the tropics, subtropics and temperate regions (with the exception of Australia, New Zealand and Europe) and easily distinguished from other Neotropical Urticaceae by the combination of opposite leaves and a single ligulate intrapetiolar stipule in each leaf axil. Most of the species are small shade-loving forest herbs, many of which are facultatively epiphytic or epipetric.

The last comprehensive treatment of the genus was that of Weddell (1869), in which 159 species and three species groups, *Integifoliae*, *Heterophyliae* and *Dentatae*, were recognized. Since that time many new species have been described; *Index Kewensis* (Anon., 1997) lists 813 species names worldwide, and estimates for the number of species range from 500 (Adams, 1970) to 600 (Burger, 1977). Subsequent to Weddell's 1857 and 1869 revisions, the majority of contributions to the taxonomy of the genus have come from flora treatments, with major additions to neotropical *Pilea* made by Killip (1936, 1939), Standley & Steyermark (1952), Adams (1972), and Burger (1977).

While preparing a revisionary account of *Pilea* for *Flora Mesoamericana*, 2042 collections from Central and South America were examined and seven new species described by the author (Monro, 1999). A further three new species are identified here. In the absence of a phylogenetic analysis of *Pilea*, the position of the new taxa in relation to Weddell's species groups is indicated after each species description.

***Pilea conjugalis* A.K. Monro, sp. nov.** Type: Panama, Chiriquí, humid forest between Alto de las Palmas and top of Cerro de la Horqueta, 2100–2268 m, 18 March 1911, Pittier 3230 (NY!—holotype).

Fig. 1.

Species *P. pittieri* Killip similis, sed floribus staminatis minimis, stipulis minimis, fructibus maioribus, differt.

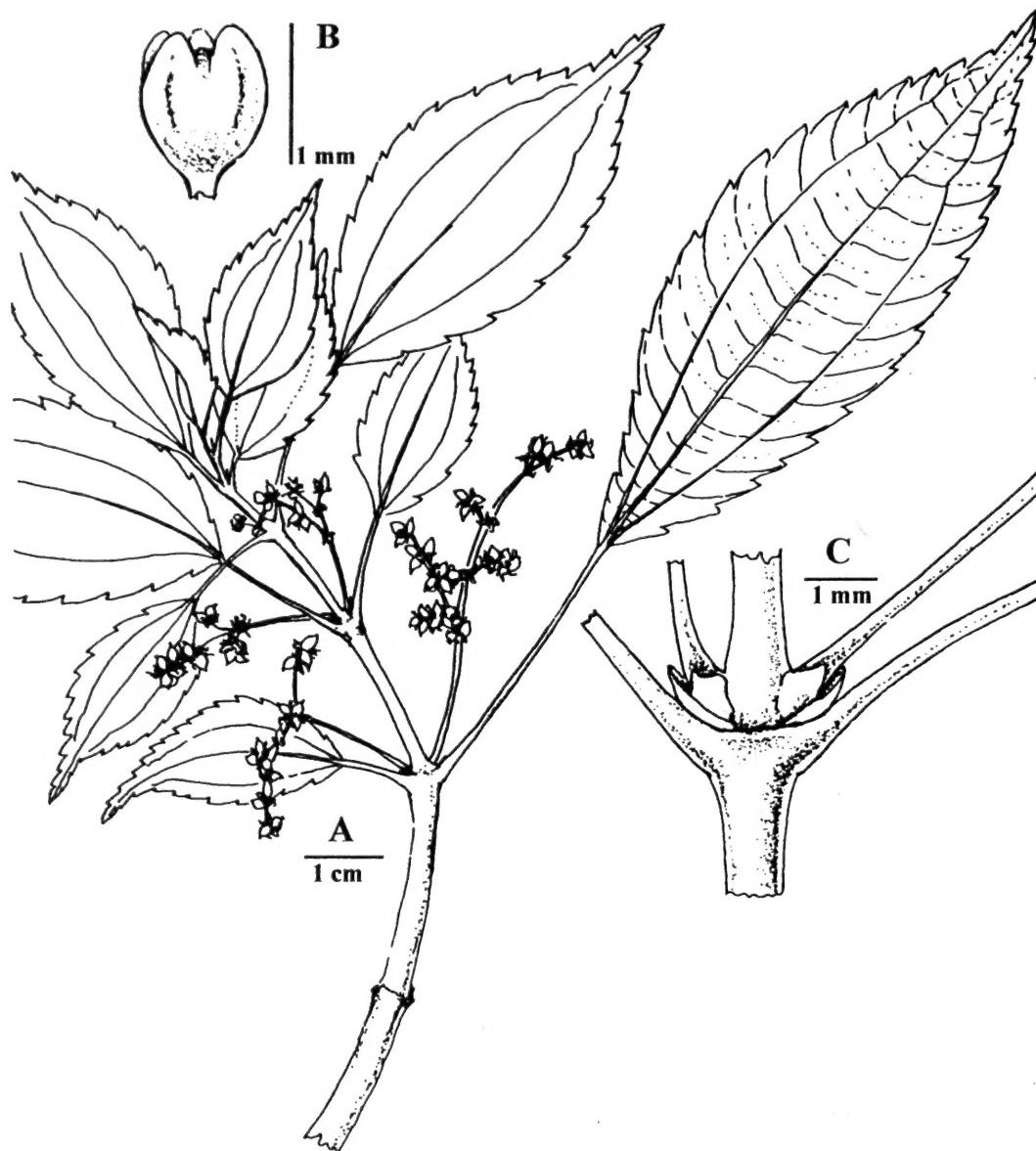
*Herb* to 60 cm, perennial; terrestrial, monoecious. *Stems* erect, branched, rooting at the base; internodes 9–55 × 0.8–4.0 mm, weakly striate, drying dark brown to black, glabrous, without cystoliths. *Stipules* 1.0–2.5 × 1.0–1.5 mm, deltate, membranous, brown, persistent. *Laminae of leaves* at the same node unequal in length by ratio 1:1.5–3.0, petiolate, the major leaves 32–121 × 10–40 mm, elliptic to ovate, subchartaceous to chartaceous; adaxial surface drying brown to dark brown, glabrous, cystoliths fusiform,

occasionally elliptic; abaxial surface drying brown to grey-brown, glabrous, cystoliths fusiform and occasionally disc-shaped, punctate-glandular; base asymmetrical or symmetrical, acute, obtuse or subcordate; margin serrate, frequently denticulate towards the apex of the lamina, with basal  $\frac{1}{5}$  to  $\frac{1}{8}$  entire; apex symmetrical, acuminate; primary venation 3-veined, the two lateral veins stopping short of the lamina apex, secondary veins 12–39 pairs, 75–90° to the midrib; the minor leaves 16–52 × 8–20 mm, otherwise as major leaves. *Inflorescences* 6–20 per stem, bisexual or unisexual, where bisexual dominated by one sex; peduncle and pedicels subtended by stipuliform bracts, the peduncular bracts 1.0–1.5 mm, ovate, the pedicellar bracts 0.4–0.5 mm, narrowly deltate to subulate. *Staminate and staminate-dominated inflorescences* solitary, 12–68 mm, bearing 15–300 flowers in a loose panicle; peduncle  $\frac{1}{3}$  to  $\frac{2}{3}$  inflorescence length, 0.5–0.8 mm in diameter, glabrous; pedicels 0.5–0.8 × 0.2–0.3 mm, glabrous; flowers in bud immediately prior to anthesis 1.0–1.5 × 0.8–1.5 mm, pale brown; tepals 4, c. 1.0–1.5 mm, elliptic to obovate, glabrous, the subapical appendages 0.3–0.5 mm, ridge-like, glabrous; stamens 4, filaments 1.3–1.8 mm, anthers 0.8–1.0 × 0.5–1.0 mm. *Pistillate and pistillate-dominated inflorescences* solitary, 29–33 mm, bearing 44–100 flowers in a loose panicle; peduncle  $\frac{1}{3}$  to  $\frac{2}{3}$  inflorescence length, 0.5 mm in diameter, glabrous; pedicels 0.2–0.5 × 0.2 mm, glabrous; flowers 0.7–1.0 × 0.4–0.5 mm, glabrous; tepals 3, unequal, glabrous, the central one 0.5–0.8 mm, oblong to obovate, with a dorsal appendage, the lateral two, 0.5–0.8 mm, asymmetrically ovate, each with a dorsal appendage. *Infuctescences* 24–70 × 0.5–0.8 mm; fruit 1.8–2.0 × 1.3–1.5 mm, asymmetric, compressed elliptic to ovoid, cream to pale brown, the ventral margin broadest at the apex, the dorsal margin narrow, thickened.

**DISTRIBUTION.** North and central Costa Rica and western Panama at 1500–2300 m, in premontane and montane wet forest.

## MATERIAL EXAMINED.

**COSTA RICA.** Alajuela: Atlantic side of Alto Palomo, 1900 m, Lent 1818 (F). Cartago: c. 15 km S. of Tapantí along the new road, on E. slope above Río Grande de Orosi near the concrete bridge, 09°42'N 83°47'W, 1500 m, Burger & Liesner 6799 (F, MO); Tapantí Reserve, 1400–1700 m, Gómez 19272 (BM); c. 6 km S. of Cartago by air, Quebrada Cangreja, 3 km S. of Pan American Highway, 09°46'N 83°57'W, 1620–1650 m, Liesner & Judziewicz 14487 (BM); N. and S. slopes of ridge on eastern side of Río Grande de Orosi, opposite mouth of Río Humo, c. 6 km upstream from Tapantí, 09°43'N 83°47'W, 1500–1800 m, Grayum et al. 4532 (BM); c. 15 km S. of Tapantí along the new road, on E. slope above Río Grande de Orosi near the concrete bridge, 09°42'N 83°47'W, 1500 m, Burger & Gentry 9192 (F); c. 10 km S. of Tapantí along the new road on E. slope above Río Grande de Orosi, 09°42'N



**Fig. 1** *Pilea conjugalis* (Pittier 3230, NY). A. Fertile branch with infructescences, B. Staminate flower immediately prior to anthesis, C. Stipules.

83°47'W, 1400–1600 m, *Burger & Stolze* 5715 (F); c. 10 km S. of Tapantí along the new road on E. slope above Río Grande de Orosi, 09°42'N 83°46'W, 1600 m, *Burger & Burger* 7568 (BM, F). **HEREDIA:** saddle between Volcán Barva and Volcán Irazú, headwaters of Río Patria, 2200 m, *Godfrey* 66148a (MO); ridges and steep slopes along the Río Para Blanca, Cerros de Zurquí, 10°03'N 84°01'W, 1600–1800 m, *Burger et al.* 10244 (F, MO); Río Vueltas (upper Río Patria) on E. slope of Volcán Barva on Caribbean side of continental divide, 10°06'N 84°04'W, 1900 m, *Burger & Gentry* 9029 (F, MEXU, NY); road between San Rafael and Río Las Vueltas, along Río Patria above bridge, 10°05'N 84°04'W, 2020–2040 m, *Stevens* 13929 (BM, MO); along headwaters of Río Santo Domingo, c. 3 km E. of San Rafael de Vara Blanca, N. slope of Volcán Barva, 10°11'N 84°07'W, 2060 m, *Grayum* 7106 (BM); Río Vueltas (upper Río Patria), E. slope of Volcán Barva near continental divide, 10°06'N 84°04'W, 2000 m, *Barringer & Christenson* 3379 (F); base of Cerro Zurquí, 10°03'N 84°02'W, 1600 m, *Lent* 3572 (F).

**PANAMA. Chiriquí:** Cerro Pata de Macho, c. 5 miles NE of Boquete, trail to continental divide leading to Finca Serrano, *Antonio* 2638 (MO); 7 km

NW of Cerro Punta, Las Nubes region, 7200 ft, *Hammel* 1439 (MO); trail to Cerro Pate Macho, headwaters of Río Palo Alto, above Palo Alto, 1700–2100 m, 08°47'N 82°22'W, *Knapp et al.* 4256 (MO); c. 0.5 km E. of Cerro Pate Macho, headwaters of Río Palo Alto, 08°47'N 82°21'W, 1800–2100 m, *Knapp et al.* 2114 (MO); above Guadalupe, c. 2 km N. of Cerro Punta, 2200 m, 08°53'N 82°33'W, *Maas & Dressler* 4842 (F); vicinity of Las Nubes, 2.7 miles NW of Río Chiriquí Viejo W. of Cerro Punta, 2200 m, *Croat* 22383 (GH).

This species falls into Weddell's *Heterophyllae* species group (with leaves of unequal length at each node). *Pilea conjugalis* most closely resembles *P. pittieri* Killip from Costa Rica. It may be distinguished from the latter by stipule shape and size, staminate inflorescence arrangement, and staminate and pistillate flower morphology, as summarized below.

*Pilea pittieri*: stipules 3–18 mm, oblong or obovate, caducous;

staminate flowers borne in 1–5 compact heads, the flowers 2–3 mm; fruit 0.8–1.5 mm.

*Pilea conjugalis*: stipules 1.0–2.5 mm, deltate, persistent; staminate flowers borne in a loose panicle, the flowers 1.0–1.5 mm; fruit 1.8–2.0 mm.

Many collections of *Pilea conjugalis* have been identified as *P. gracilipes* Killip, a species ranging from southern Mexico to northern South America. Although there is a similarity in leaf shape and margin, *P. gracilipes* differs in stem colour, leaf isomorphy, staminate inflorescence arrangement, and fruit size, as summarized below.

*Pilea gracilipes*: stem drying grey-green to green; leaves of equal or subequal length at each node, where subequal by a ratio less than 1:1.5; staminate flowers borne in a compact head; fruit 1.3–1.5 mm.

*Pilea conjugalis*: stem drying dark brown to black; leaves of unequal length at each node by ratio 1:1.5–3.0; staminate flowers borne in a loose panicle; fruit 1.8–2.0 mm.

The species epithet refers to the presence of both male and female flowers on the majority of the inflorescences encountered, an infrequent, although not rare, occurrence in the genus *Pilea*.

***Pilea adamsiana* A.K. Monro, sp. nov.** Type: Panama, Veraguas, mountains west of Alto de Piedras Junior High School north of Santa Fe, Cerro Arizona (highest peak visible west of school), 1000–1450 m, 11 September 1978, Hammel 4702 (MO!-holotype). Fig. 2A–C.

Species *P. pallida* Killip similis, sed habitu epiphytico, folii margine discrete crenulato, fructibus maioribus, differt.

*Shrublet* or *herb* to 30 cm, perennial; epiphytic, monoecious. *Stems* repent, sparsely branched, rooting at the base and adventitiously; internodes 6–34 × 1.8–4.0 mm, weakly striate, drying dark brown to grey-brown, glabrous, cystoliths fusiform. *Stipules* 1.5–3.5 × 1.0–1.5 mm, deltate, membranous to subchartaceous, grey to brown, persistent. *Laminae of leaves* at the same node of equal length or subequal, petiolate, 23–115 × 8–27 mm, oblanceolate or obovate, chartaceous to subcoriaceous; adaxial surface drying dark brown, glabrous, cystoliths fusiform, rarely 'V'-shaped; abaxial surface drying red-brown or grey-brown, glabrous, cystoliths fusiform, disc-shaped, rarely 'V'-shaped, punctate-glandular; base symmetrical, cuneate, occasionally weakly subcordate; margin crenulate, basal  $\frac{2}{3}$  to  $\frac{3}{4}$  entire; apex symmetrical, cuspidate; primary venation 3-veined, the two lateral veins stopping short of the lamina apex, secondary veins 7–33 pairs, 75–90° to the midrib; petioles equal or subequal, 7.5–25 × 0.8–1.8 mm, glabrous. *Inflorescences* 2–16 per stem, unisexual, pistillate inflorescences preceding staminate inflorescences; peduncle and pedicels subtended by stipuliform bracts, the peduncular bracts 1.3–2.0 mm, deltate, the pedicellar bracts 0.5–1.0 mm, narrowly deltate to subulate. *Staminate inflorescences* 1–2 per axil, 15–35 mm, bearing 60–200 flowers in a single compact head; peduncle  $\frac{1}{2}$  to  $\frac{2}{3}$  inflorescence length, 0.5–0.8 mm in diameter, glabrous; pedicels 1.0–4.0 × 0.3–0.4 mm, glabrous; flowers in bud immediately prior to anthesis 2.5–3.5 × 0.8–1.3 mm, brown; tepals 4, 3–4 mm, elliptic, glabrous, the subapical appendages 1.5–2.0 mm, narrowly oblong to elliptic, frequently reflexed, glabrous; stamens 4, filaments 1.5–2.5 mm, anthers 1.0 × 1.0 mm. *Pistillate inflorescences* 1–2 per axil, c. 7 mm, bearing 24–40 flowers in a semi-compact panicle; peduncle  $\frac{1}{2}$  to  $\frac{2}{3}$  inflorescence length, c. 0.5 mm in diameter, glabrous; pedicels c. 0.8 × c. 0.4 mm, glabrous; flowers c. 1.3 × c. 0.8 mm, glabrous; tepals 3, unequal, the central one c. 1.0 mm, oblong to spatulate, not dorsally thickened, the lateral two c. 0.8 mm, oblong to spatulate, not dorsally thickened. *Infuctescences* 12–26 × 0.5–0.8 mm; fruit 1.8–2.3 × 1.3–1.4 mm, asymmetrical,

compressed, elliptic, pale brown to brown, the ventral margin broadest towards the apex and flattened, the dorsal margin narrow, thickened.

**DISTRIBUTION.** Known only from the Cerro Tute in Veraguas, western Panama, at an altitude of 1300–1500 m, growing on tree branches in premontane and montane wet forest.

#### MATERIAL EXAMINED.

**PANAMA.** Veraguas: vicinity of Escuela Agricultura Alto Piedra near Santa Fe, trail to top of Cerro Tute, 1400 m, Antonio 2010 (MO); vicinity of Escuela Agricultura Alto Piedra near Santa Fe, trail to top of Cerro Tute, 1400 m, Antonio 2014 (MO); Cerro Tute ridge up from former escuela Agrícola, Santa Fe, 08°35'N 81°05'W, 1400–1450 m, Hamilton & Krager 4010 (MO).

This species falls within Weddell's *Integrifoliae* species group (with leaves of equal length at each node and entire margins). *Pilea adamsiana* A.K. Monro most closely resembles *P. pallida* Killip from Costa Rica and Panama. It may be distinguished from the latter by its habit, leaves, indumentum, staminate inflorescence, and fruit, as summarized below.

*Pilea pallida*: terrestrial; leaves ovate, falcate, lanceolate; leaf margin prominently serrate, basal  $\frac{1}{5}$  to  $\frac{1}{3}$  of the leaf entire; staminate peduncle  $\frac{1}{8}$  inflorescence length; fruit 0.8–1.0 mm.

*Pilea adamsiana*: epiphytic; leaves oblanceolate or obovate; leaf margin discretely crenulate, basal  $\frac{2}{3}$  to  $\frac{3}{4}$  of the leaf entire; staminate peduncle  $\frac{1}{2}$  to  $\frac{2}{3}$  inflorescence length; fruit 1.8–2.3 mm.

*Pilea adamsiana* is named after C.D. Adams, whose previous work on the genus and assistance with the *Flora Mesoamericana* account have proved invaluable.

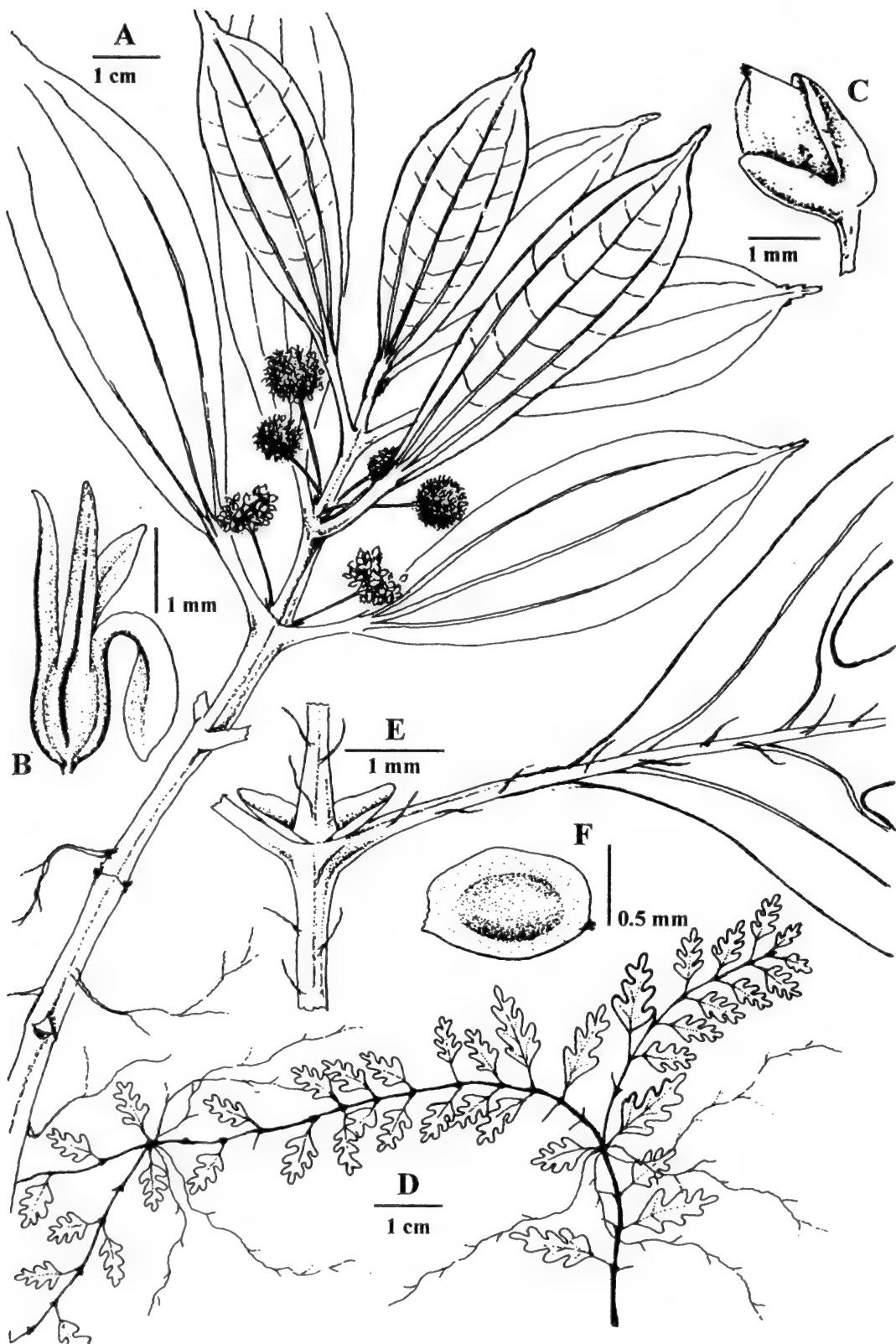
***Pilea trichomanophylla* A.K. Monro, sp. nov.** Type: Panama, Bocas del Toro, La Fortuna area, Gualaca to Chiriquí Grande, along oil pipeline road along continental divide W. of road, 1300 m, 08°45'N 82°17'W, 6 March 1986, Hammel et al. 14646 (MO!-holotype). Fig. 2D–F.

Species foliis pinnatilobatus a congeneribus diversa.

*Herb* to 5 cm, perennial; epipetric. *Stem* repent, little branched, rooting at the base and adventitiously; internodes 4.5–12 × 0.4–0.8 mm, weakly striate, drying dark brown to black, sparsely pubescent, the hairs to 0.8 mm, weakly appressed, crooked or curved, cystoliths fusiform. *Stipules* 0.8–1.5 × 1.0–1.3 mm, auriculate, membranous, dark brown, persistent. *Laminae of leaves* at the same node of equal length or subequal, petiolate, 5.0–13.5 × 2.5–7.0 mm, ovate, pinnately lobed, membranous; adaxial surface drying green to brown-green, sparsely pubescent, the hairs to 0.5 mm, appressed, curved, cystoliths fusiform; abaxial surface drying grey-green, sparsely pubescent, the hairs to 0.5 mm, appressed, straight or curved, cystoliths absent, eglandular; base symmetrical or asymmetrical, decurrent and/or cuneate; margin entire; apex symmetrical, obtuse; primary venation pinnate, secondary veins 3–5 pairs, visible, 60° to the midrib; petioles unequal in pair by ratio 1:1.5–3.0, the major 2.5–4.0 × 0.3 mm, the minor 1.0–2.5 mm, sparsely pubescent, the hairs to 0.5 mm, erect, crooked. *Inflorescences* and intact *infuctescences* not seen. *Fruit* 0.8–1.0 × 0.5 mm, asymmetrical, subcompressed, elliptic, brown, the margin broad, thickened.

**DISTRIBUTION.** Known only from the type collection from Chiriquí, Panama, growing at 1300 m on a rock face at the base of a waterfall.

This species falls into Weddell's *Dentatae* species group (with leaves of equal length at each node and toothed margins). *Pilea trichomanophylla* is named after its very distinctive leaves and habit



**Fig. 2** A–C. *Pilea adamsiana* (Hammel 4702, MO). A. Fertile branch with staminate inflorescences and infructescences, B. Staminate flower immediately prior to anthesis, C. Fruit. D–F. *Pilea trichomanophylla* (Hammel et al. 14646, MO). D. Fertile branch, E. Stipules, F. Fruit.

(Fig. 2D) which closely resemble those of some filmy ferns of the genus *Trichomanes*. It is the unmistakable nature of its leaves and the fact that it resembles no other known species from the neotropics which gives the author the confidence to publish this name as a new species despite the absence of flowers on the specimen. There is a remote possibility that the collection on which this description is based is of a precociously fertile plant of an already named species, the unusual leaf shape representing a developmental dimorphism. But this is deemed unlikely, and if it were the case, the sole species with the combination of repent form, small stipules, and isomorphic, toothed, pubescent leaves is *P. nummulariifolia* (Sw.) Wedd., and this species is not known from Cerro Tute, being typical of more open vegetation such as pine-oak formations. There are also morphological differences in stem colour, stipule texture and size, and leaf indumentum which would not be expected in a developmental dimorphism.

**ACKNOWLEDGEMENTS.** I thank Helen Greenop for preparing the illustrations, Norman Robson and Denis Adams for help with translating the Latin diagnoses, and Karen Sidwell and Bob Press for helpful comments on the

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# A revision of *Solanum thelopodium* species group (section *Anthoresis* sensu Seithe, pro parte): Solanaceae

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**SYNOPSIS.** The *Solanum thelopodium* species group, as delimited here, includes three species of slender, wand-like shrubs of primary rainforest in Amazonia and northern South America. All of the species inhabit the dark forest understory, and two of the three occur exclusively in Amazonia. Two new species are described, *S. monarchostemon* of Amazonian Colombia, Ecuador and Peru, and *S. dimorphandrum* of N. and W. coastal Colombia and adjacent Panama. The group is defined by an unusual zygomorphic androecium, which is not found anywhere else in the genus *Solanum*. The nomenclature and morphology of the group is examined in detail, with particular emphasis on the unusual androecium and seeds. Although the phylogenetic position of the group is not known at present, it is possibly related to sections *Pachyphyllea*, *Cyphomandropsis* and *Allophyllum* of *Solanum* subgenus *Solanum*.

## INTRODUCTION

Despite being one of the five or six largest genera of flowering plants, *Solanum* L. (Solanaceae) has been the focus for relatively little monographic work (see D'Arcy, 1991). The genus is diverse, with some 1000 or more valid species (D'Arcy, 1991), but monographs do not exist for the majority of species groups in *Solanum*. Taxonomic research effort has been concentrated on groups of economic importance, such as potatoes, tomatoes, nightshades, and selected groups of the spiny solanums (see Knapp, 1989; Knapp & Helgason, 1997 for references). As part of an ongoing research program into the taxonomy and phylogeny of non-spiny solanums (see Knapp, 1986, 1989, 1991a; Knapp & Helgason, 1997) I have

investigated the unusual, primarily rainforest species allied to *S. thelopodium* Sendtn. The group, whose members are characterized by a ternately branched, terminal inflorescence and markedly dimorphic anthers, consists of just three species, and is morphologically very different from any other group of solanums. I have called this group the *Solanum thelopodium* species group, following the convention of Whalen (1984) for recognition of infrageneric groups in *Solanum*. Several potential sister groups have been identified; these will be treated in future monographs, and larger scale relationships tested as more monophyletic groups are identified. This is the first study to define species limits in the *S. thelopodium* species group and to examine its phylogenetic position within the larger scope of *Solanum*.

## TAXONOMIC AND NOMENCLATURAL HISTORY

*Solanum* is most species-rich in the New World tropics and subtropics, and thus many of the taxa have been described relatively recently. The last comprehensive treatment of the genus was by Dunal (1852) and while 900 species were treated in the *Prodromus*, at least 4000 specific epithets exist for *Solanum* at present. By convention and for convenience *Solanum* is usually divided into two main groups, the spiny solanums (subgenus *Leptostemonum*) and the non-spiny solanums (the rest: subgenera *Solanum*, *Brevantherum*, *Bassovia*, *Archaeosolanum*, *Lyciosolanum* and *Potatoe* – D'Arcy, 1972, see Table 1). Taxonomy of non-spiny solanums has long been confused, and there is considerable disagreement as to the circumscription of monophyletic groups within that portion of the genus (Bohs & Olmstead, 1997; Olmstead & Palmer, 1997). For a detailed history of the taxonomy of *Solanum* both before and after Dunal (1852) see Knapp (1989, 1991a) and Bohs (1994). Knapp (1989) also provides a list of recent monographs of sections of *Solanum*, to which can be added a monograph of *Solanum* section *Allophyllum* (Child) Bohs (Bohs, 1990), the genus *Cyphomandra* (Bohs, 1994; now with all epithets transferred to *Solanum*, see Bohs, 1995), and *Solanum* section *Pteroidea* Dunal (Knapp & Helgason, 1997).

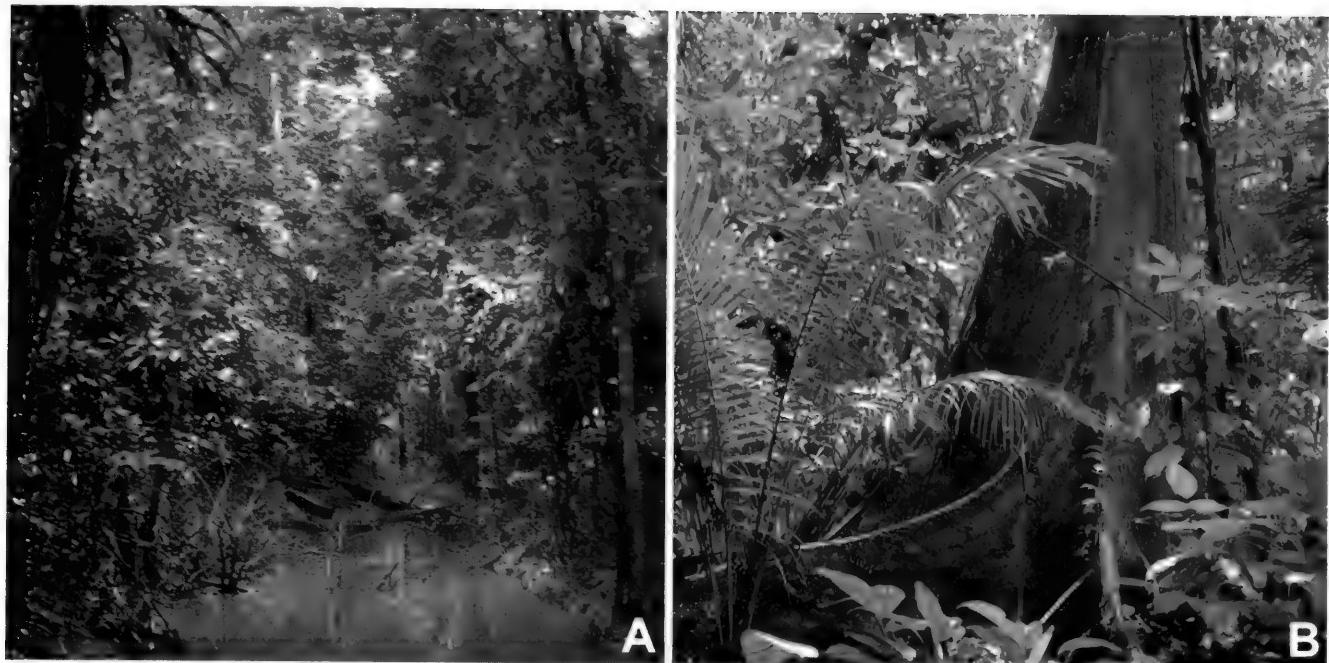
Since its description by Otto Sendtner in 1846, *Solanum thelopodium* has been enigmatic. Morphologically very distinct from other non-spiny solanums (see below), it has been placed in section *Anthoresis* (Dunal) Bitter by the only two authors to specifically consider it, Dunal (1852) and Seithe (1962). The great early twentieth century solanologist Georg Bitter thought *S. thelopodium* was distinct enough to merit generic rank, but although he annotated herbarium sheets accordingly (e.g. Ule 5691 in HBG), he never published the name.

In his group (grad. ambig.) *Anthoresis*, Dunal included 77 species

of solanums with terminal and later lateral inflorescences and terminal poricidal anthers where the pores were oval ['Racemi, corymbi, cymae vel paniculae terminales, dein laterales. Antherarum pori antici ovales magni, nonunquam minutti orbicularis.']. Included in the group were species of currently recognized sections *Geminata* (G. Don) Walp., *Afrosolanum* Bitter, *Madagascarienses* Bitter, *Lepidotum* Seithe, *Brevantherum* Seithe, members of the *Solanum nitidum* species group, and some members of subgenus *Leptostemonum*. Although Dunal included *S. thelopodium* in his group *Anthoresis*, he had never seen a specimen and went entirely on Sendtner's description. Seithe (1962) lectotypified section *Anthoresis* with *Solanum cervantesii* Lag. (= *Solanum pubigerum* Dunal) and defined the group as shrubs and subshrubs with entire leaves, terminal or lateral inflorescences and unisexual or branched trichomes. Species she included in the group were various members of the *Solanum sessile* species group (section *Geminata* s.s., see Knapp, 1991a, b), members of the *Solanum nitidum* species group (see Knapp, 1989), members of section *Holophylla* (G. Don) Walp. s.s. (see below) and *Solanum thelopodium*. Gilli (1970) followed Seithe's system almost exactly, using section *Anthoresis*, but never listed any component species in his groups, so the utility of his classification is limited. His section *Anthoresis* is defined largely on geography, as being composed of species from Central and South America. Danert (1970) correctly realized that section *Holophylla* was the correct sectional name for the group containing Seithe's lectotype species, *S. cervantesii*, but did not specifically mention *S. thelopodium* in his description and delimitation of the group. His concept of section *Holophylla* is essentially the same as that of Seithe, but he mentions that the species are grouped together for convenience, and perhaps belong to several different groups. D'Arcy (1972) superfluously lectotypified both section *Anthoresis* and section *Holophylla* with *Solanum pulverulentum* Pers. (= *S. nitidum* Ruiz & Pav.: see Knapp, 1989), thereby confusing the situation somewhat. However, since Seithe's lectotypification has priority,

Table 1 Traditional classification of *Solanum* (after D'Arcy, 1972).

Subgenus	Characters	Sections included by D'Arcy, 1972	Monophyly: Bohs & Olmstead, 1997
<i>Solanum</i>	stout anthers, simple hairs, no spines	<i>Solanum</i> , <i>Afrosolanum</i> Bitter, <i>Benderianum</i> Bitter, <i>Chamaesarachidium</i> Bitter, <i>Episarcophyllum</i> Bitter, <i>Gonatotrichum</i> Bitter, <i>Leiodendra</i> (= <i>Geminata</i> ) Dunal, <i>Lemurisolanum</i> Bitter, <i>Lysiphellos</i> (Bitter) Seithe, <i>Macronesiotes</i> Bitter, <i>Quadrangulare</i> Bitter	no
<i>Bassovia</i>	stout anthers, simple hairs, pinnate leaves, axillary inflorescences, pointed fruits	<i>Pteroidea</i> Dunal, <i>Herpestichum</i> Bitter, <i>Herposolanum</i> Bitter	not included in analysis
<i>Brevantherum</i>	stout anthers, entire leaves, dendritic or stellate hairs	<i>Brevantherum</i> Seithe, <i>Extensum</i> D'Arcy, <i>Holophylla</i> (G. Don) Walp., <i>Lepidotum</i> Seithe, <i>Pseudocapsicum</i> Bitter	no
<i>Potatoe</i>	scandent species, pinnate leaves with interstitial leaflets, lateral pendulous inflorescences, articulated pedicels	<i>Petota</i> Dumort., <i>Anarrhichomenum</i> Bitter, <i>Basarthrum</i> (Bitter) Bitter, <i>Dulcamara</i> Dumort., <i>Jasminosolanum</i> Seithe, <i>Neolycopersicon</i> Corr., <i>Normania</i> (Lowe) Bitter, <i>Regmandra</i> (Dunal) Ugent, <i>Rhynchantherum</i> Bitter	no
<i>Leptostemonum</i> The 'spiny solanums'	tapering anthers, stellate hairs, often spines	see Whalen, 1984	no
<i>Lyciosolanum</i>	stout anthers, rotate flowers, elongate filaments (South Africa)	<i>Lyciosolanum</i> Bitter	not included in analysis
<i>Archaeosolanum</i>	stout anthers, rotate flowers, aneuploid chromosome numbers (Australia)	<i>Archaeosolanum</i> Danert	yes



**Fig. 1** Habitats of the *Solanum thelopodium* species group. A. Tahuampa or flooded forest, B. Non-flooded forest. Both from Peru: Loreto: Yanamono, Rio Amazonas between Indiana and mouth of Rio Napo.

we must now regard section *Holophylla* (see discussion in Knapp, 1989) as including only those species related to *Solanum cervantesii* (= *S. pubigerum* Dunal). *Solanum thelopodium* has always been an afterthought in all of the previous systems, as its morphology is so apparently aberrant and specimens are so few. The species, nor its two very close relatives described here, has not been included in any of the recent DNA phylogenies of the genus *Solanum* (Olmstead & Palmer, 1991; Bohs & Olmstead, 1997; Olmstead & Palmer, 1997).

## MORPHOLOGY AND NATURAL HISTORY

### Habitats

Plants of the *Solanum thelopodium* species group are generally found in or around primary forest. *Solanum thelopodium* itself is usually recorded as occurring in periodically flooded forest – igapó or tahuampa – and is occasionally recorded as being weedy at the edges of clearings. Where I have collected *S. thelopodium* and *S. monarchostemon* growing sympatrically (Yanamono, Dept. Loreto, Peru), they occupy different habitat types: *S. thelopodium* in the sunny clearings in the tahuampa and *S. monarchostemon* in the understory of primary forest (see Fig. 1A, B). Label data from specimens collected in the Ecuadorian Amazon indicate this is also the case there (Brandbyge et al. 33209, *S. thelopodium*; Brandbyge et al. 33192, *S. monarchostemon*).

### Stems

The single-stemmed growth habit of plants of the *Solanum thelopodium* species group is unusual in *Solanum*. The plants are occasionally described as branching, but label data usually mention the wand-like stems characteristic of this group. Some specimens have been collected with their roots, and these are enlarged, thick-

ened and very woody (see Fig. 2). These sorts of tap-roots appear to be more common in *S. thelopodium*, and may be related to growing in periodically flooded forests.

In all *Solanum* species the young stem is monopodial with the leaves arranged in a 2/5 phyllotactic spiral. When a given stem begins its reproductive stage, sympodial growth begins (Danert, 1958, 1967; Child, 1979, 1991; Bell & Dines, 1995). Every inflorescence is developmentally terminal and shoot continuation and elongation is initiated in the axil of the leaf subtending the inflorescence. Monochasial growth patterns result from a single lateral continuation of shoot growth, while a dichasial growth pattern results from a double lateral continuation (see Fig. 3). In general, a given species is either monochasial or dichasial (see Knapp, 1989), but occasionally both growth patterns occur on a single plant (Bell & Dines, 1995). The determining factor for pattern expression appears to be the dormancy of axillary buds in a given sympodial unit. Sympodial units in *Solanum* consist of leaves along each shoot terminating in an inflorescence, and can vary from plurifoliate (members of sections *Brevantherum*, *Holophylla*, the *S. nitidum* species group) to unifoliate (section *Pteroidea*, some species groups in section *Geminata*). The sympodial units in the *S. thelopodium* species group appear to be plurifoliate, with the most common number of leaves between inflorescences being three. However, most plants bear only a single inflorescence and thus consist of a single plurifoliate sympodial unit.

### Leaves

The leaves of members of the *S. thelopodium* species group are usually clustered at the top of the stem (see Figs 2, 7, 8, 10). They are simple, entire and elliptic to obovate in outline. Leaf size is variable both within species and within single plants. The texture is membranous, and some specimens have extremely thin leaves, particularly those from forest understory habitats. Both *S. thelopodium* and *S.*



**Fig. 2** Enlarged woody root or underground stem of *Solanum thelopodium* (S.F. Smith et al. 533, Madre de Dios, Peru).



**Fig. 3** Sympodial growth patterns in *Solanum*. A. Dichasial growth, B. Monochasial growth.

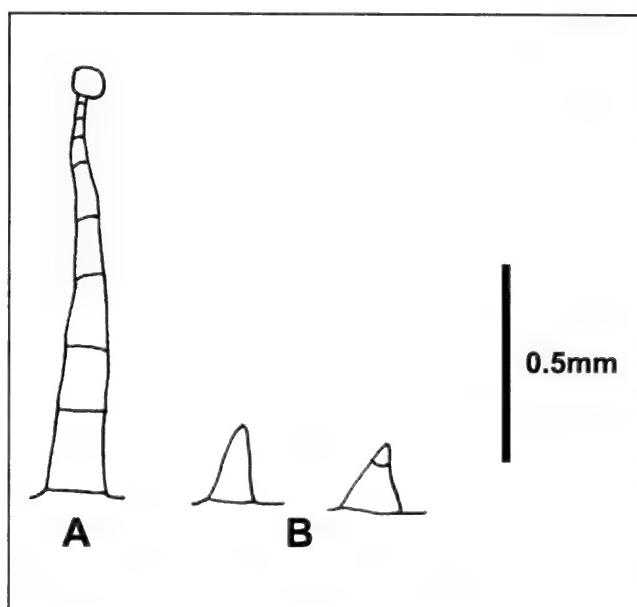
*monarchostemon* occasionally have purple or deep burgundy-red leaf undersides. This is also common in section *Pteroidea* (the *S. mite* species group, see Knapp & Helgason, 1997) and may be related to deep forest habitat, although in section *Pteroidea* populations are often dimorphic for the character.

No herbivorous insects have been observed or reported feeding on members of the *Solanum thelopodium* group (Brown, 1987; Drummond & Brown, 1987; Beccaloni, 1995), although ithomiine butterflies (Nymphalidae: Ithomiinae) commonly lay their eggs on similar understory solanums (see Knapp & Helgason, 1997). Damage on leaves of herbarium specimens however is consistent with ithomiine larval feeding, and a few specimens have the damage characteristic of feeding by chrysomelid (Coleoptera: Chrysomelidae) beetles (see Knapp, 1986 for details).

## Inflorescences

Inflorescences of the *Solanum thelopodium* species group are scorpioid cymes with the flowers arranged in two rows along the inflorescence axis. This inflorescence type is common to all *Solanum* species and is variously misinterpreted as a raceme or panicle (Dunal, 1852). In the *S. thelopodium* species group the inflorescence is always either bifurcate or ternate with an elongate, erect and rather stout peduncle. The two or three branches all arise from a single point, so the entire structure has an unusual umbrella-like appearance. Other non-spiny solanums with branched inflorescences generally have branches arising all along the length (*S. sessile* species group, see Knapp, 1991a; *S. nitidum* species group, see Knapp, 1989) or at irregular intervals on all sides of the axis (e.g. *S. terminale* Bitter of section *Afrosolanum* Bitter).

In the *Solanum thelopodium* species group, pedicel scars are present to the bases of the branches, with occasionally a single scar in the fork; flowers are never borne on the erect peduncle. The pedicels are articulated at the base and do not leave pegs (section *Pachyphylla*, see Bohs, 1994), sleeves (*S. nitidum* species group, see Knapp, 1989), 'platforms' (section *Holophylla* s.s., see Knapp, 1989) or other such prominent scars. In any given inflorescence only one flower per branch is open at a time, but each branch may bear up to 100 flowers over its lifespan. Pubescence of the inflorescence generally parallels that of the leaves, but in *S. monarchostemon*, the



**Fig. 4** Trichome types in the *Solanum thelopodium* species group. A. Long, uniseriate trichomes of *S. monarchostemon*, B. Papillate trichomes found in all species.

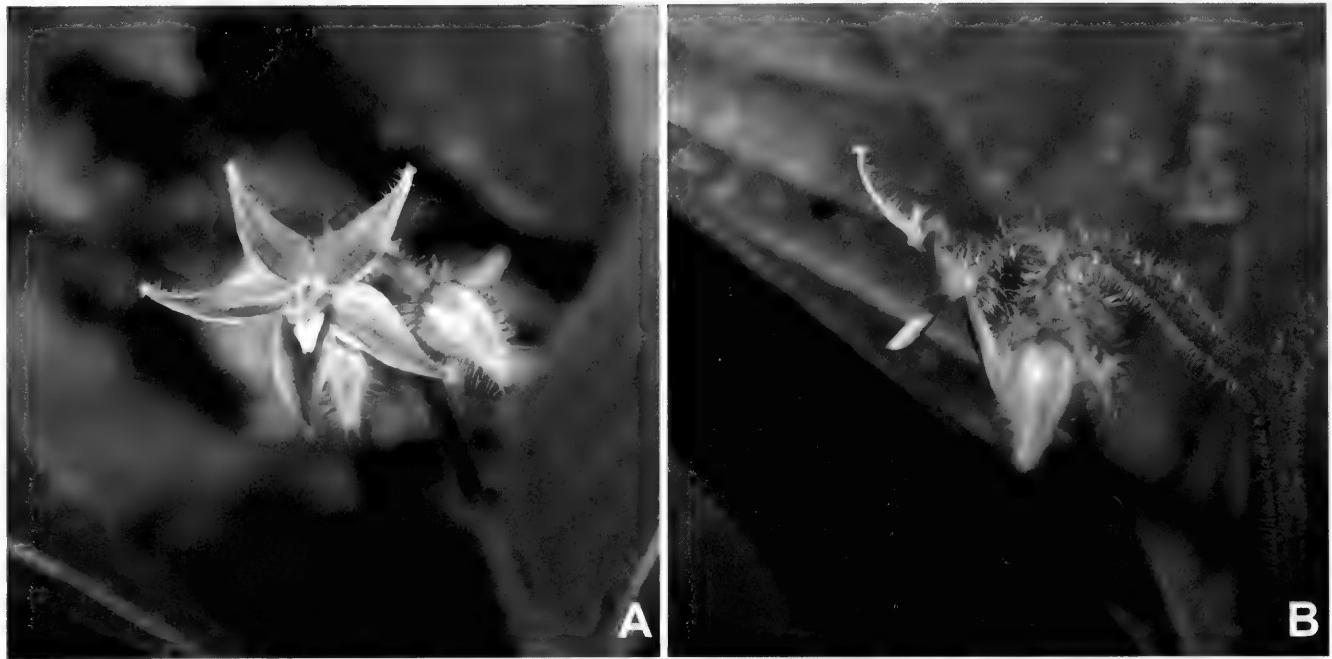
inflorescence is usually more densely pubescent than the leaves and is the most reliable place to look for trichomes.

## Trichomes

Trichome morphology traditionally has been used extensively in *Solanum* taxonomy and can be a rich source of useful characters (Seithe, 1962; Roe, 1971; Seithe, 1979; Edmonds, 1982; Seithe & Anderson, 1982; Whalen, 1984; Knapp, 1989, 1991b). Trichomes in the *S. thelopodium* species group are exclusively simple and uniseriate, varying between single-celled papillate trichomes (all three species) to multicellular, long, white, sometimes glandular, trichomes (*S. monarchostemon*). In *S. monarchostemon*, trichome density varies considerably, but there are always some long, white uniseriate trichomes (see Fig. 4) present on the inflorescence and leaf uppersides. On the leaf uppersides of *S. monarchostemon* the trichomes are present only on the lamina, while on the leaf undersides, they are present only along the veins. Specimens from the provinces of Pastaza and Sucumbíos in eastern Ecuador have inflorescence trichomes with glandular tips; the gland appears to be a single cell and usually dries a reddish brown.

## Flowers

In most species of *Solanum* the flowers are actinomorphic and pentamerous. The calyx is synsepalous and the corolla sympetalous, with a very short floral tube. Members of the *S. thelopodium* species group are unusual in the genus in having markedly zygomorphic flowers, with the zygomorphy largely due to the dimorphic anthers. In the group, the calyx lobes are deltate to quadrate. Calyx pubescence parallels that of the rest of the inflorescence, but in some collections of *S. monarchostemon*, the calyx is the most densely pubescent part of the reproductive axis. The corolla is pentamerous, and lobed nearly to the base. The corolla lobes are very narrowly triangular-attenuate, and have markedly cucullate tips. Mature buds just before anthesis are curved at the tips, reflecting this corolla lobe shape. The corolla is either pink or greenish white: plants of



**Fig. 5** Flowers of the *Solanum thelopodium* species group. A. *S. monarchostemon* front view, B. *S. monarchostemon*, side view (both Knapp 6606, Loreto, Peru).

*S. thelopodium* tend to more often have pinkish corollas, while those of *S. monarchostemon* and *S. dimorphandrum* tend to have white or greenish white corollas. Colour polymorphism, however, probably exists in all three species (only recorded in *S. thelopodium* and *S. monarchostemon*).

In all three species of the *Solanum thelopodium* group the corolla is nodding at anthesis. The corolla lobes are planar, but the pedicel is deflexed such that the plane of the corolla is at approximately 45° from horizontal (see Fig. 5). The pedicel becomes erect in fruit (Fig. 8, also see below).

The androecium is the most unusual feature of members of the *Solanum thelopodium* species group, and is found nowhere else in non-spiny solanums. In general, the androecium in non-spiny solanums is remarkably uniform, but some use has been made of relatively small differences in pore size and shape and union of filaments (Knapp, 1986; Barboza & Hunziker, 1991). These minor characters, however, can vary considerably between plants of the same species (Knapp, 1986). Some spiny solanums have strongly zygomorphic flowers with markedly dimorphic anthers (section *Androceras*, see Whalen, 1979; *S. tridynamum* Dunal), and some non-spiny solanums have one anther slightly longer than the rest (*S. pensile* Sendtn., *S. wendlandii* Hook.f.), but the situation in the *S. thelopodium* species group is unique in non-spiny solanums. Individual anthers can be classified as one of three types which I have characterized in the species descriptions as long anthers (one only), medium anthers (a pair) and short anthers (a pair). In living plants the anthers are always arranged with the long anther lowermost, the medium anthers next in sequence and the short anthers uppermost (see Figs 5, 8). The anthers thus closely invest the style, which is held in the connective groove of the long anther (see below). The two pairs of anthers (medium and short) are morphologically like those of other non-spiny solanums: ellipsoid in shape, they are poricidally dehiscent with ovate, terminal pores. Unlike other species of non-spiny solanums, however, the pores do not markedly elongate

gate to slits with age, but remain round. The connective of these four anthers is somewhat prolonged at the tip, forming an apiculus which can be as long as 0.5 mm in some individuals. In any individual flower the medium pair of anthers is usually somewhat longer and larger than the short pair, but within a species, measurements overlap completely (see species descriptions). The difference in appearance is almost entirely due to filament length. Filaments on the medium pair are longer than those of the short pair (see Fig. 8). The filament of the long anther is even longer, and is usually almost twice as long as the filaments of the short anther pair. The long anther is somewhat different morphologically from the others. It is larger than the other four, triangular in shape with an elongate tip and wide base (see Fig. 8), slightly paler yellow, and has an unusual membranous connective, wider than the two thecae, in which the style is held at anthesis. The pores at the tips are rounded and extremely small, and the connective is somewhat pointed and prolonged at the tip beyond the pores.

The flowers of all species of *Solanum* are buzz pollinated by bees (Buchmann, 1983): the anthers are tightly grasped by the bee who vibrates her indirect flight muscles, causing pollen to be released in a cloud and deposited on the underside of the thorax and abdomen. In solanums with isomorphic anthers the bee's body is positioned directly over the centre of the anther cone, and the anthers are all manipulated in a similar way. In those taxa with dimorphic anthers, such as members of *Solanum* section *Androceras* (i.e. *S. rostratum* Dunal and relatives), the long anther is differently coloured (usually flushed with purple) and is not manipulated by the bee, who vibrates and 'milks' the cone of four anthers (Bowers, 1975; Whalen, 1979). In section *Androceras*, the long anther functions in pollination while the other anthers are largely the source of 'feeding pollen' for visiting bees. I have not seen flower visitors to any of these species, nor are any reported on labels or in the literature, so how this anther arrangement functions in pollination in the *S. thelopodium* species group is not known. The paler colour of the long anther, coupled

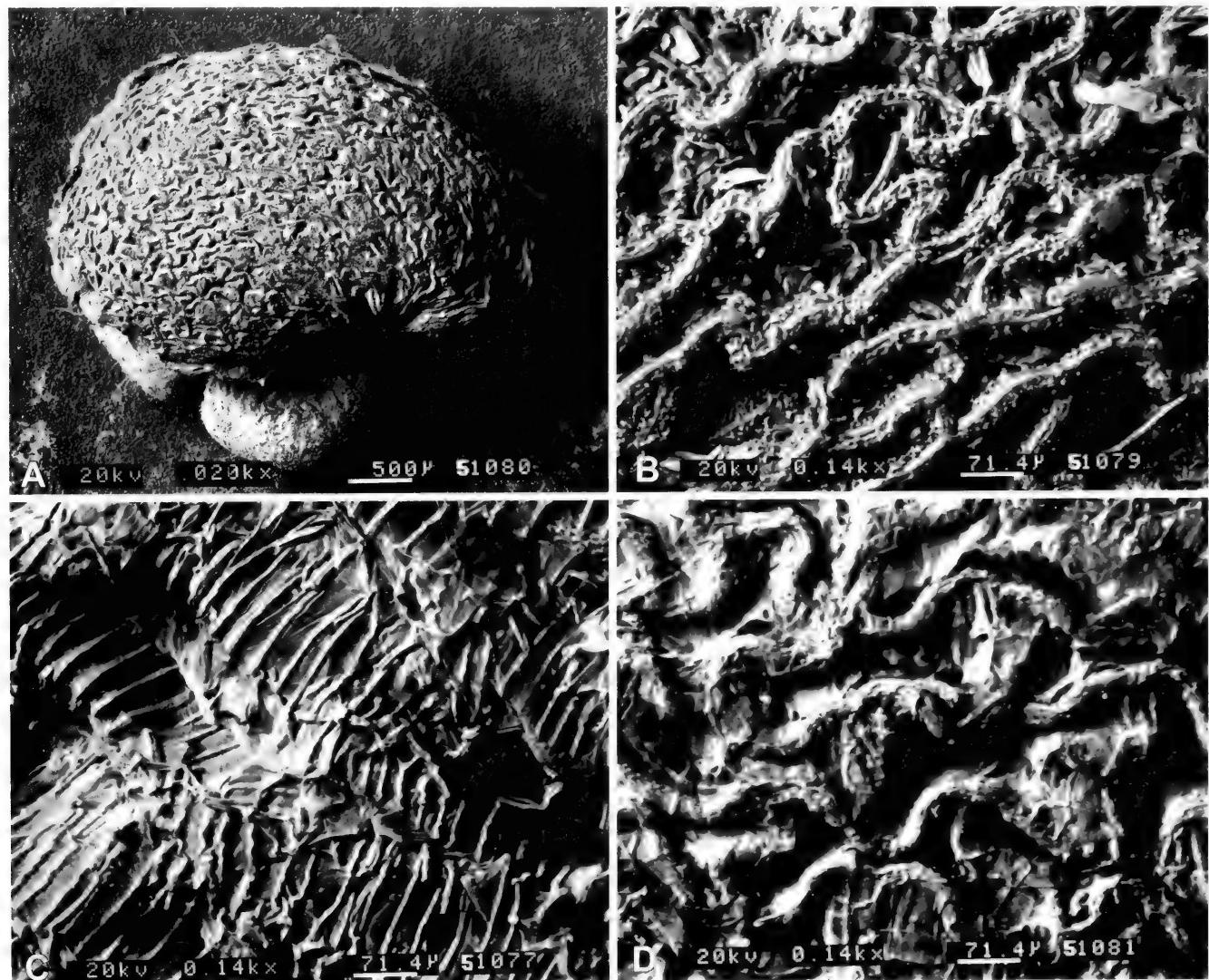
with the tight connivence of the other four in a cone suggests a similar mechanism to that found in the spiny solanums is operating, however.

The ovary is bilocular, conical and glabrous. The style is glabrous, slightly curved, and at anthesis held in the groove of the connective of the large anther. The stigma is flattened and somewhat capitate, and not particularly large. Members of the *Solanum thelopodium* species group do not appear to ever bear short-styled flowers, unlike many groups of non-spiny solanums (see Knapp, 1986; Whalen & Costich, 1986; Knapp & Helgason, 1997). Pollen grains for the group are not known at present, but are being investigated as part of a wider study on anther morphology in the non-spiny solanums. They are likely, however, to be tricolporate with a granular exine as are all other members of the genus *Solanum* (Anderson, 1977; Punt & Monna-Brands, 1980; Bohs, 1994; Knapp et al., 1998).

## Fruits and seeds

The most common fruit type in *Solanum* is a berry, although other

modified fruit types are found, particularly in Australia (Symon, 1979). Members of the *S. thelopodium* species group all have smooth berries that remain green at maturity. *Solanum thelopodium* and *S. monarchostemon* have globose berries, while *S. dimorphandrum* has ellipsoid berries. Some specimens of *S. thelopodium* have somewhat ellipsoid immature berries, but at maturity the berries are globose. The pointed apex of berries of *S. dimorphandrum* is seed-bearing, rather than being sterile as is often the case in the apiculate berries of section *Pteroidea* (see Knapp & Helgason, 1997). Berries of members of the *S. thelopodium* species group have distinctive dark green stripes when mature, usually four stripes at right angles to one another. The pericarp of berries of all three species is extremely thin when mature, and in dry material quite brittle. At maturity the fruits are held erect on thickened pedicels, but when immature the fruits are nodding as were the flowers (see above). Nothing is known about fruit and seed dispersal in this group, but the soft berries on erect pedicels that remain green at maturity suggest either bats or small mammals as dispersal agents.



**Fig. 6** Seeds of the *Solanum thelopodium* species group. A. Whole seed of *S. dimorphandrum* (Forero et al. 4071), B. Sinuate cells (outer testa removed) of *S. monarchostemon* (Palacios & Neill 649), C. Outer testal wall with conspicuous and regular thickenings ('comb-like') of *S. monarchostemon* (Gentry et al. 54613), D. Outer testal wall lacking conspicuous and regular thickenings of *S. dimorphandrum* (Forero et al. 4071).

Seed morphology has proved useful in *Solanum* taxonomy (Edmonds, 1983; Lester & Durrants, 1984; Bohs, 1994; Knapp & Helgason, 1997) and patterns of testal wall thickenings and cell shape are quite variable in the genus. All three members of the *S. thelopodium* species group have relatively few seeds per fruit (5–20). Some other non-spiny solanum groups, such as some species groups of section *Geminata*, also have few seeds per fruit, but many other solanums have large numbers of seeds in each berry (i.e. most spiny solanums, the members of section *Solanum*, the potatoes, tomatoes and their relatives, members of section *Pachyphyllea*, etc.).

All three species of the group have reddish brown seeds that are reniform in outline and somewhat ovoid, rather than being markedly flattened as are many other *Solanum* seeds. The fine structure of seeds has been useful for resolving the relationships among species where morphological characters exhibit complex and overlapping patterns of variation. In Solanaceae, lateral cell wall structure can be seen after enzymatic digestion of the outer cell wall (Lester & Durrants, 1984). In order to examine cell wall structures, seeds were collected from herbarium specimens, washed in distilled water and air dried, and photographed using a ISI ABT-55 low vacuum scanning electron microscope. The lateral cell walls of these seeds do not consist of 'hairs' (see Souèges, 1907; Lester & Durrants, 1984; Edmonds, 1983; Bohs, 1994; Knapp & Helgason, 1997), but are thickened and in all three species the cells are sinuate in outline (see Fig. 6). In *S. thelopodium* and *S. monarchostemon*, but not in *S. dimorphandrum*, the outer testal wall has conspicuous, regularly spaced comb-like thickenings (see Fig. 6), which disappear with vigorous seed cleaning and thus would probably not survive enzymatic digestion.

## RELATIONSHIPS

### Relationships of the group within *Solanum*

*Solanum thelopodium* and its relatives are superficially so morphologically different from other members of the genus *Solanum* that a new genus was proposed (but never published) for them by Georg Bitter in the early years of this century (Bitter, in litt.). These differences, particularly in the structure of the androecium, are clearly autoapomorphic, and although indicating the monophyly of this small group, tell us nothing about its relationships to the rest of *Solanum*. Sendtner (1846), Dunal (1852), and Seithe (1962) by placing *S. thelopodium* in groups containing other species with branched, terminal or lateral inflorescences, clearly felt that its affinities lay with these taxa. The taxa placed in section *Anthoresis* (= *Holophylla*) are now considered to be members of various other groups, all of which may have some relationship to the *S. thelopodium* species group (see Table 2 for a list of putative sister groups of the *S. thelopodium* species group). Other groups of solanums which may

**Table 2** Possible sister groups for the *Solanum thelopodium* species group.

Group or section	Shared characters
section <i>Allophylla</i>	tightly connivent anthers, woody habit
section <i>Pachyphyllea</i>	tightly connivent anthers, modified connective
section <i>Geminata</i> ( <i>S. sessile</i> species group)	woody habit, pseudoterminal branched inflorescences
section <i>Cyphomandropsis</i>	woody habit, tightly connivent anthers, enlarged rootstocks
section <i>Holophylla</i> s.s.	woody habit, branched inflorescences

be related to the members of the *S. thelopodium* species group are sections *Pachyphyllea* (ex *Cyphomandra*), *Cyphomandropsis* and *Allophyllum*, all of which have variously modified androecia (see Bohs, 1989, 1994). None of the taxa of the *S. thelopodium* species group have been included in DNA phylogenies of *Solanum*, and potential sister taxa fall into two separate clades (see Bohs & Olmstead, 1997). Future analyses of anatomy, morphology (Knapp, in prep.) and DNA sequences (Bohs, pers. comm.) will certainly shed light on the placement of this unusual group in *Solanum*.

### Relationships of the species

Within the group, *Solanum thelopodium* and *S. monarchostemon* share a number of morphological characters (globose fruit at maturity, seeds with striate outer testal wall, small flowers), perhaps indicating they are sister taxa, more closely related to each other than either is to *S. dimorphandrum*. The long, white, uniseriate trichomes (occasionally gland-tipped) of *S. monarchostemon* are autapomorphic in the group, as are the ellipsoid fruits of *S. dimorphandrum*. Rigorous cladistic analysis of the relationships of these three species is more appropriately done in the wider context of the entire genus *Solanum*, where appropriate hypotheses can be made concerning character polarity within and among other lineages in the genus.

## TAXONOMIC TREATMENT

### Key to selected groups of non-spiny solanums (woody plants, shrubs or subshrubs)

- 1 Inflorescences appearing axillary or in branch forks ..... 2
- Inflorescences appearing lateral or leaf-opposed ..... 4
- 2 Plants small trees or shrubs, branching in a complex crown; inflorescences in branch forks; anthers with an enlarged, thickened connective ..... *Solanum* section *Pachyphyllea* (genus *Cyphomandra*)
  - Plants wand-like, shrubs, vines, or herbaceous; inflorescences only in leaf axils; anthers without an enlarged, thickened connective ..... 3
  - 3 Trailing herbs, rooting at the nodes, inflorescences with a single flower; fruit with smooth surfaces ..... *Solanum* section *Herpestichum*
    - Upright herbs, slender shrubs or vines, inflorescences many (up to 30)-flowered; fruit smooth or rugose ..... *Solanum* section *Pteroidea*
  - 4 Inflorescences internodal ..... 5
  - Inflorescences leaf-opposed or terminal ..... 7
  - 5 Flowers small, the anthers not markedly connivent, oblong, with large pores; fruits with thin pericarp, stone cells usually present ..... *Solanum* section *Solanum*
    - Flowers larger, the anthers tightly connivent, tapered distally, with small pores; fruits with pericarp various, often green at maturity, stone cells usually absent ..... 6
  - 6 Inflorescences unbranched; fruit often laterally compressed ..... *Solanum* section *Allophyllum*
    - Inflorescences branched; fruit not laterally compressed ..... *Solanum* section *Cyphomandropsis*
  - 7 Pedicel scars flush with the rachis ..... *Solanum thelopodium* species group
    - Pedicel scars variously raised ..... 8
  - 8 Pedicel scars in sleeves ..... *Solanum nitidum* species group
    - Pedicel scars on platforms ..... *Solanum* section *Holophylla* s.s.

## The *Solanum thelopodium* species group

*Solanum* grad. ambig. *Anthoresis* Dunal in A. DC., *Prodr.* 13(1): 29, 95 (1852), pro parte, excluding lectotype species. Lectotype species: *Solanum cervantesii* Lag. (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (D'Arcy, 1972).

*Solanum* section *Anthoresis* (Dunal) Bitter in *Bot. Jb.* 54: 489 (1917), excluding lectotype species. Lectotype species: *Solanum cervantesii* Lag. (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (D'Arcy, 1972).

**Shrubs** or slender herbs, usually single-stemmed, 0.2–1(–1.5–2) m tall; pubescence of papillate or uniseriate simple trichomes; stems monochasial. *Sympodial units* plurifoliate, the number of leaves per unit extremely variable, the inflorescences usually terminal and with no further lateral growth. *Leaves* elliptic to obovate, glabrous or pubescent with simple, uniseriate trichomes above and beneath. *Inflorescences* terminal or pseudoterminal, bifurcate or ternate, the branches all arising from a single point, papillate or pubescent with usually uniseriate trichomes like those of the leaves, the peduncle stout, usually longer than the branches; pedicels at anthesis white or greenish white, deflexed; buds elliptic when young, later strongly curved and pointed, variously pubescent; *calyx* tube usually conical, the lobes minutely deltoid or long-triangular and acuminate; *corolla* white, greenish white, occasionally pink, or tinged with purple, membranous, lobed nearly to the base, the lobes planar at anthesis, narrowly triangular, the tips and margins of the lobes usually densely papillate, the tips cucullate; *anthers* strongly unequal, one pair on short filaments, one pair on medium length filaments, the anthers of these anther pairs elliptic to obovate, the fifth anther much larger than the rest, with a broad flattened connective, yellow or orangish yellow, all anthers poricidal at the tips, the pores not elongating to slits; *ovary* glabrous; *style* curved and sitting in the groove formed by the connective of the large anther, glabrous; *stigma* capitate or restricted to the unexpanded tip of the style. *Berries* globose or somewhat ellipsoid, bi-locular, usually green or yellowish green at maturity, often with four distinct green lines or blotches from tip to base; *fruiting pedicels* erect, usually thicker at the apex; *seeds* flattened to ovoid-reniform without incrassate margins, the lateral seed coat walls lignified, the outer testa walls with or without regular, comb-like thickenings. *Chromosome number*: not known for any of the three species.

This revision is based on herbarium specimens and field observations. Taxa in the *Solanum thelopodium* species group are extremely rare and poorly collected and I have cited every herbarium specimen I have seen. The species are delimited on morphological grounds, with ecological and geographical differences being taken into account where appropriate.

Photographs of type specimens are cited in the recommended manner (see Knapp, 1989, 1991a; Knapp & Helgason, 1997), with the negative number cited in square brackets. Herbaria in possession of prints of that negative are also included in the brackets. Copies of these negatives are generally available from the institutions where they are housed: F for F negatives and US for Morton negatives.

Herbaria are cited using the acronyms in *Index herbariorum* (Holmgren et al., 1990) and types seen are indicated by an exclamation mark (!). I have seen all non-type specimens cited in the species accounts, unless otherwise indicated.

## Key to species of the *Solanum thelopodium* species group

1. Plants with at least some long, white uniseriate trichomes (to 3 mm long) on the inflorescences; leaves pubescent above ..... **2. *S. monarchostemon***  
Plants with no long, white uniseriate trichomes on the inflorescences, the pubescence of short, papillate trichomes; leaves glabrous above ..... **2**
2. Fruit ellipsoid; outer testal cell walls not markedly or regularly striate; NW South America and Panama ..... **1. *S. dimorphandrum***  
Fruit globose; outer testal cell walls markedly and regularly striate; Amazonia, often in flooded forests ..... **3. *S. thelopodium***
1. ***Solanum dimorphandrum* S. Knapp, sp. nov.** Type: Colombia, Magdalena, Sierra Nevada de Santa Marta, Valparaíso, '4500 ft.', 28 February 1899, H.H. Smith 1190 (NY!-holotype; GH!, K!, MO!, US!-isotypes).

Fig. 7

*Solanum anceps* of D'Arcy, 1974['1973'] not of Ruiz & Pavón.

Species *Solanum thelopodium* Sentner affinis, sed floribus grandibus, baccis ellipsoidibus, cellulis testaceis non striatis, differt.

Suffruticose herbs to shrubs, 0.5–1.5(–2) m, single-stemmed; stems glabrous; bark reddish brown. Leaves 11.5–45 × 4.5–20 cm, elliptic to ovate, with 7–10(–16) pairs of primary veins, glabrous on both surfaces or with very sparsely scattered uniseriate trichomes on the lamina above, not on the veins, papillate on the veins beneath; base abruptly attenuate; apex acuminate; petiole 0.9–2.5 cm. Inflorescence 2 or 3 times branched, minutely papillate, the peduncle 2–10 cm, the branches 1.5–8 cm, with a single flower open at a time, but with up to 100 scars, the scars beginning at the fork. Buds elliptic, becoming pointed before anthesis. Pedicels 0.9–1 cm, papillate, deflexed. Flowers with the calyx tube conical to flattened, c. 1 mm, the lobes broadly deltate, 0.5–1 mm, densely to sparsely papillate, without an apical tuft of trichomes; corolla green or white, 1.5–2 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, 8–9 mm, narrowly triangular, the tip markedly cucullate, densely papillate on tips and margins; filament tube absent; long anther 3–5 × c. 1 mm, the filament c. 1.5 mm; middle anther pair 3–3.5 × c. 1 mm, the filaments c. 1 mm; small anther pair 2.5–3.5 × c. 1 mm, the filaments c. 0.5 mm; ovary conical, glabrous; style 4–7 mm, glabrous, the stigma minutely flattened capitate. Fruit ellipsoid, 1.6–1.9 × 1–1.2 cm, green with four darker stripes, smooth, the pericarp thin and brittle when dry; fruiting pedicel 1.2–1.4 cm, erect. Seeds 10–15 per fruit, 4–6 mm long, pale tan or reddish, flattened reniform, the testal cells sinuate in outline, without regularly striate outer cell walls, the thickenings, if present, irregular and sparse.

COMMON NAMES AND USES. Colombia, Bolívar: 'raicilla de agua' (Pennell 4204).

DISTRIBUTION. In low to mid elevation forests on the northern and western coasts of Colombia and adjacent Panama, 0–1000(–1750) m. (Fig. 8).

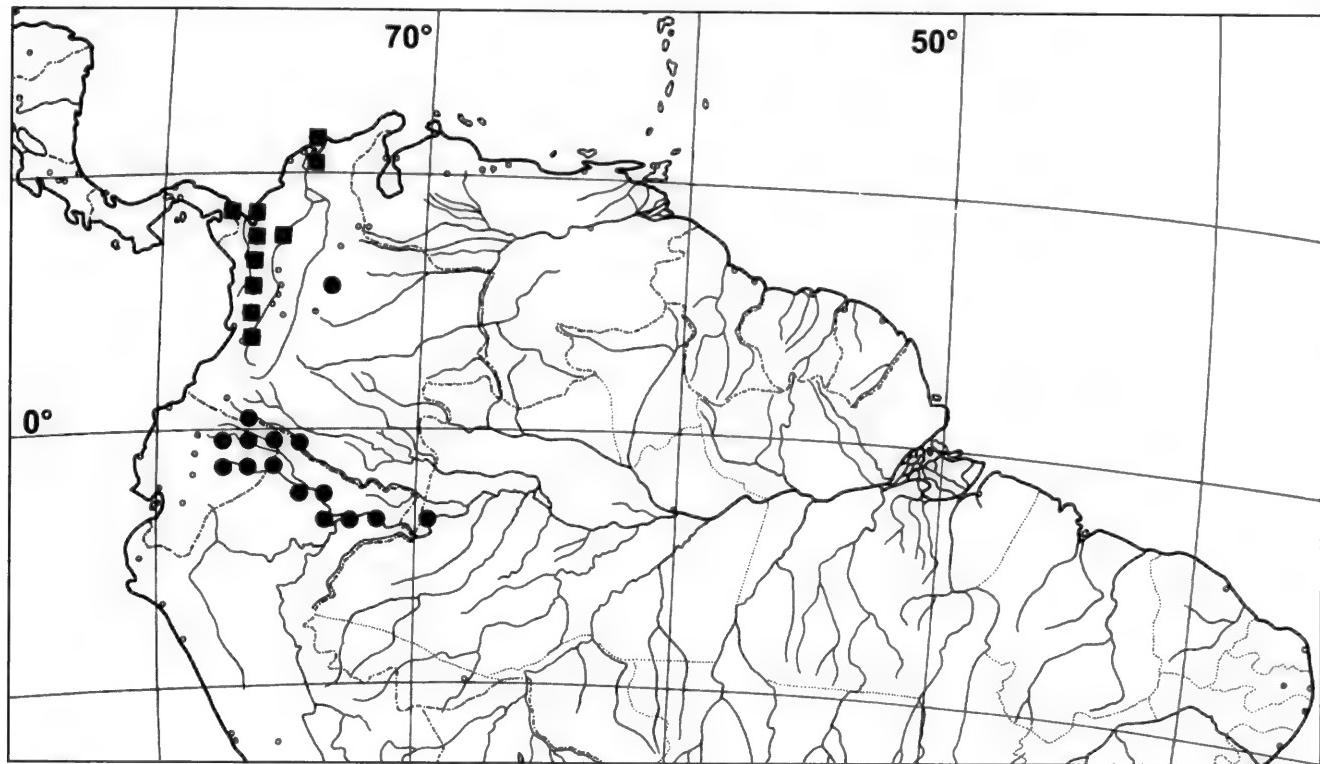
### SPECIMENS EXAMINED.

**PANAMA. Darién:** 10 km NE of Jaque, headwaters of Río Pavarandó, 1400 ft, 31 January 1981, D'Arcy & Sytsma 14515 (MO); Boca de Pavarandó on Sambú River, 1911, Pittier 5585 (F); Cerro Pirre, just S. of Pirre, 10–20 July 1977, Folsom 4524 (MO); vicinity of Cerro Tacaruna summit camp, 1500–1750 m, 31 January 1975, Gentry & Mori 14041 (MO). **San Blas:** SE of Puerto Obaldía, 18 August 1971, Croat 16769 (MO).

**COLOMBIA. Antioquia:** Parque Nacional Natural Las Orquídeas, sector



Fig. 7 Holotype of *Solanum dimorphandrum* (Smith 1190, Magdalena, Colombia).



**Fig. 8** Distribution of *Solanum dimorphandrum* (squares) and *S. monarchostemon* (circles).

Venados arriba, L. bank of Río Venados, 1110–1240 m, 6°34'N, 76°19'W, 27 July 1988, Cogollo et al. 3536 (MO); Chigorodo, 40 km S. of Turbo, c. 50 m, 22 May 1945, Haught 4702 (NY, US); Quebrada Mercedes, E. of Turbo, c. 75 m, 14 July 1946, Haught 4963 (US x 2); road to sea near Villa Arteaga, 150 m, 4–8 August 1947, Hodge 7075 (US); Mun. de Carepa, 2 km N. of Carepa, grounds of ICA at Tulenapa, 20 m, 7°52'N, 76°42'W, 25 March 1987, Zarucchi et al. 4994A (MO). **Bolívar:** Boca Verde, on Río Sinú, 100–300 m, 13–14 February 1918, Pennell 4204 (NY). **Chocó:** Mun. de Quibdó, Corregimiento de Guayabal, Río Hugon, c. 80 m, 12 September 1976, Forero & Jaramillo 2795 (MO, NY); Río San Juan drainage, small hill in front of Palestrina, 30–40 m, 4°10'N, 77°10'W, 26 March 1979, Forero et al. 4071 (MO); Río Atrato, between Loma del Sapo & Bocas de Guayabal, about 20 mins upriver from Quibdó by motorboat, 40 m, 23 June 1983, Forero et al. 9450 (MO); Río Taparal off Río San Juan, 100 ft, 24 August 1962, Hugh-Jones 329 (K); S. of Río Condoto, between Quebrada Guarapo & Mandinga, 120–180 m, 22, 28 April 1939, Killip 35131 (US). **Magdalena:** Sierra Nevada de Santa Marta, above Finca Reflejo, Quebrada La Sierra, 1500–1800 m, c. 10°59'N, 74°01'W, 6 September 1962, Kirkbride 2122 (NY); Sierra Nevada de Santa Marta, below Las Nubes, 4250 ft, May 1899, Smith 1722 (K, NY). **Valle de Cauca:** Mun. Buenaventura, region of Bajo Calima, along road between Buenaventura & Malaga, at km 51.3, c. 100 m, 4°09'N, 77°11'W, 27 February 1990, Croat 71005 (MO); Cordillera Occidental, banks of Río Calima, El Cairo, between Darién & Mediaciona, 1650–1750 m, 6, 7 January 1943, Cuatrecasas 13928 (F); Cordillera Occidental, W. slopes, drainage of Río Sanquimí, L. bank, La Laguna, 1250–1400 m, 10–20 December 1942, Cuatrecasas 15689 (F).

*Solanum dimorphandrum* differs from both *S. monarchostemon* and *S. thelopodium* in its larger, apparently more fleshy, flowers and in its ellipsoidal berries. Like *S. thelopodium*, the leaves are glabrous or with merely papillate trichomes. *Solanum dimorphandrum* tends to grow at slightly higher elevations than the other two taxa, and is only found north and west of the Andes rather than in the Amazon basin.

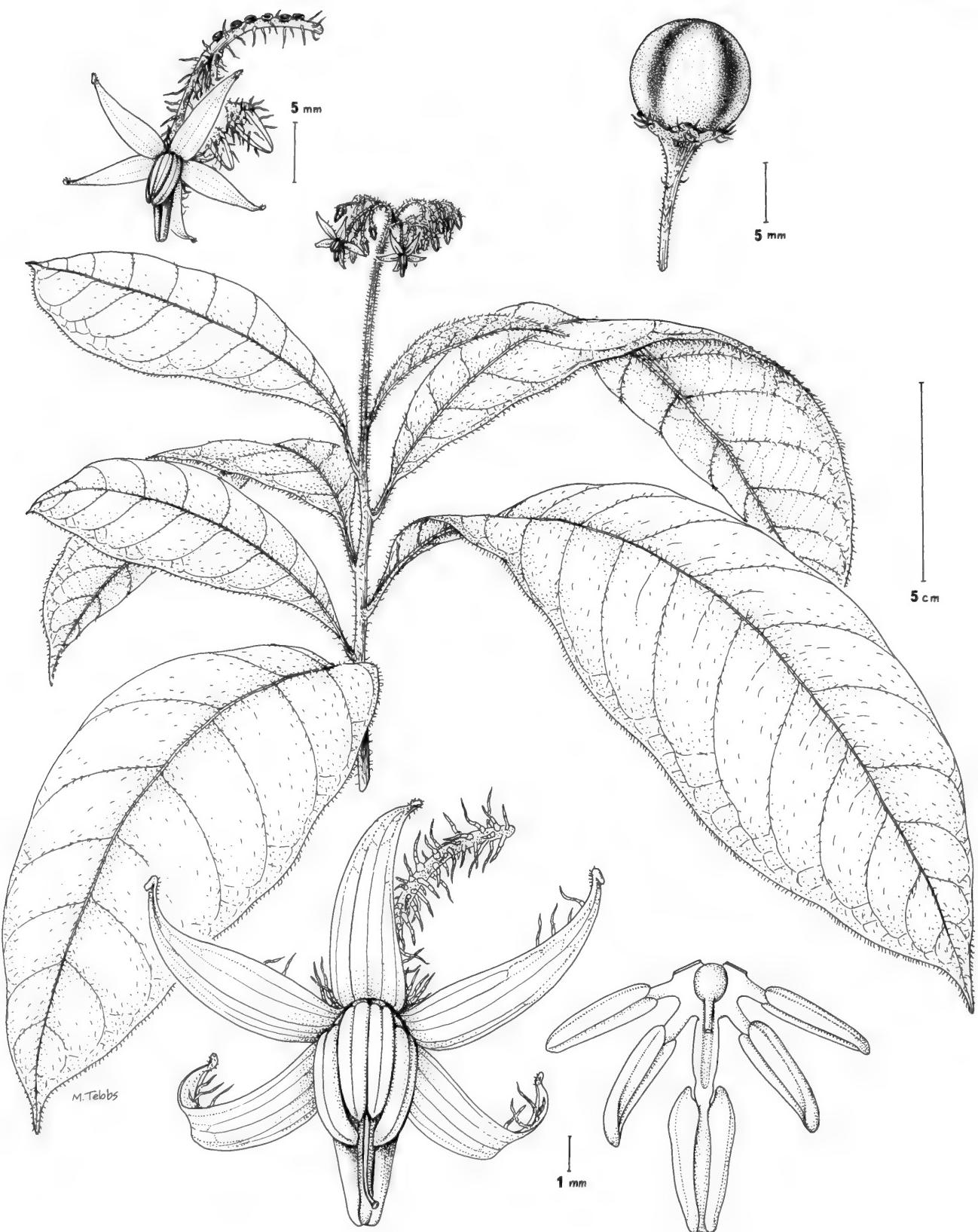
Specimens of *Solanum dimorphandrum* form the basis for the report of *S. anceps* Ruiz & Pav. from Panama (D'Arcy, 1974, but see Knapp & Helgason, 1997). *Solanum anceps*, a member of section *Pteroidea* (*S. mite* species group), is a similar simple-leaved forest subshrub, but has axillary inflorescences bearing minute flowers with a regular, radially symmetrical androecium and wrinkled, turbinate fruits (see Knapp & Helgason, 1997).

**2. *Solanum monarchostemon* S. Knapp, sp. nov.** Type: Ecuador, Pastaza, Puyo, Comunidad Santa Cecilia, Villano, 380 m, 1°30'S, 77°27'W, 1 May 1992, Palacios 10117 (QCNE!-holotype; MO!-isotype).

Fig. 9.

Species *Solanum thelopodium* Sendtner affinis, sed foliis supra et inflorescentiis pubescentibus, trichomatibus longiusculus simplicibus uniseriatibus albis, bacca minoribus differit.

*Herbs* to small shrubs, 0.5–1.3 m, single-stemmed; stems densely pubescent when young with uniseriate white trichomes, 0.5–2 mm, later glabrescent; bark brown. Leaves 9–25 × 4–10 cm, elliptic, with 8–13 pairs of primary veins, pubescent above with scattered 4–5-celled, white, uniseriate trichomes 1–2 mm long on the veins and lamina, densely to sparsely pubescent beneath with 4–7-celled, white, uniseriate trichomes 1–2 mm long, only along the veins, not on the lamina, the trichomes denser on the new growth, mixed with papillate trichomes on new growth, occasionally uniseriate trichomes glandular, the gland a single cell. Inflorescence 2 or 3 times branched from a single point, densely or more rarely sparsely pubescent with mixed papillate trichomes and uniseriate, white trichomes 1–3 mm long, these occasionally gland-tipped, the gland a single cell, the peduncle 4–9 cm, the branches 1–3 cm, each branch with a single



**Fig. 9** *Solanum monarchostemon* (based on Palacios 10117 (QCNE), Pastaza, Ecuador; fruit (immature) from Lutelyn et al. 8703 (NY)); flower details based on spirit collections of Holm-Nielsen et al. 19867, 20178 (AAU).

flower open at a time, but with up to 100 scars on each branch. *Buds* pointed, pubescent with uniseriate white trichomes. *Pedicels* (3)–5–8 mm, sparsely pubescent with uniseriate trichomes like the inflorescence or with only papillate trichomes, deflexed. *Flowers* with the calyx tube conical, 0.5–1 mm, the lobes deltate with lighter hyaline margins, 1–1.5 mm, without a distinct apical tuft of trichomes, sparsely to densely pubescent with uniseriate trichomes 0.5–2 mm long, these denser along the midline of each lobe; corolla white to greenish white, occasionally purplish tinged, 1.2–1.6 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, 6–9 mm, narrowly triangular with pointed, strongly cucullate tips, papillate at the tips or with scattered uniseriate white trichomes on the abaxial surface; filament tube minute, c. 0.1–0.2 mm; long anther 4–4.5 × c. 1.5 mm, the filament 1–1.5 mm; middle anther pair 3–3.5 × c. 1 mm, the filaments c. 1 mm; small anther pair 2.5–3 × c. 1 mm, the filaments c. 0.5 mm; ovary conical, glabrous; style 5–6 mm, glabrous, the stigma flattened capitate. *Fruit* globose, 0.8–1.4 cm in diameter, green with four darker stripes, smooth, the pericarp thin and brittle when dry; fruiting pedicel 0.8–1.8 cm, erect, or slightly deflexed from the weight of the fruit. *Seeds* 5–10(–15) per fruit, 3–3.5 mm long, pale tan or reddish, flattened to ovate-reniform, the testa cells sinuate in outline, with markedly and regularly striate outer cell walls.

**COMMON NAMES AND USES.** Ecuador, Sucumbíos, Cofán, ‘Saomatéye’hue’, Secoya, ‘aíquë’je’ (*Jaramillo & Coello* 2748); Peru, Loreto, Secoya, ‘yanse mat yna’ (*King* 472), ‘manucari’ (*Williams* 709).

**DISTRIBUTION.** In Amazonian Colombia, Peru and Ecuador, usually growing in *terra firme* (non-flooded) forests, 100–450(–1300) m. Fig. 8.

#### SPECIMENS EXAMINED.

**COLOMBIA. AMAZONAS:** Parque Nacional Natural Amacayacu, Quebrada de Agua Pudre, c. 1.5 km NE of outlet to Río Amacayacu, 200–220 m, 3°47'N, 70°15'W, 15 November 1991, *Pipoly* 16210 (MO). **BOYACÁ:** 130 miles N. of Bogotá, 3500–4000 ft, 2 March 1933, *Lawrance* 643 (K, NY).

**ECUADOR. NAPÓ:** Añangu, S. bank of Río Napo 95 km downstream from Coca, 300 m, 0°32'S, 76°23'W, 19 June–4 July 1985, *Balslev* et al. 60545 (AAU), 11–28 April 1986, *Balslev* et al. 62224, 62357 (AAU); Parque Nacional Yasuni, pozo petrolero Daimi 2, 200 m, 0°55'S, 76°11'W, 26 May–8 June 1988, *Cerón & Hurtado* 4111 (QCNE, MO); Canton Aguarico, PN Yasuní, lagunas de Garza Cocha, 200 m, 1°01'S, 75°47'W, 22 September 1988, *Cerón & Gallo* 5049 (MO); 1.1 km E. of Río Conejo on road to Lago Agrio, c. 340 m, 31 March 1972, *Dwyer & MacBryde* 9787 (MO); Río Yasuni, c. 60 km upriver from Nuevo Rocafuerte, 13 September 1977, *Foster* 3620 (F); Río Coca, 3–4 km from the mouth, c. 350 m, 11 February 1974, *Harling & Andersson* 11897 (MO); Río Yasuní, 3–4 km from Río Napo, 260 m, 0°57'S, 75°25'W, 25 August 1979, *Holm-Nielsen* et al. 19867 (AAU); 3 km E. of village of Huamán, N. of Hollin-Loreto road on trail, 1200 m, 0°43'S, 77°36'W, 17 September 1988, *Hurtado & Alvarado* 255 (MO); Nuevo Rocafuerte, SE of town, trail to Río Braga, 200–230 m, 1 March 1981, *Jaramillo & Coello* 4484, 4487 (AAU); Añangu, NW corner of Parque Nacional Yasuní, c. 300 m, 0°32'S, 76°22–23'W, 1–30 October 1983, *Korning & Thomsen* 47055, 47072 (AAU); Añangu, Río Napo, 260–350 m, 9–10 March 1983, *Lawesson* et al. 39367 (AAU); Armenia Viejo at Río Napo, c. 12 km SW of Coca (Puerto Francisco de Orellana), 12 January 1973, *Lugo* S. 2642 (MO); PN Yasuní, Anango, 0°30'S, 76°25'W, 15 July 1982, *Luteyn* et al. 8703 (NY); Orellana, road to Pozos Gacela, Gacela 2, 250 m, 0°30'S, 77°08'W, 8 August 1993, *Palacios* 11038 (MO, QCNE). **PASTAZA:** Lorocachi, 3 km S. of military camp, 200 m, 1°38'S, 75°58'W, 23 May 1980, *Brandbyge & Asanza* C. 30663 (AAU); Ceilán, pica from Ceilán to Río Coconaco on N. side of Río Curaray, 200 m, 1°36'S, 75°40'W, 6 June 1980, *Brandbyge & Asanza* C. 31653 (AAU); Río Curaray, S. bank, vicinity of Laguna Garzayacu, 250 m, 1°29'S, 76°39'W, 20–26 August 1985, *Palacios & Neill* 649 (MO). **SUCUMBÍOS:** Reserva del Batallón de la Selva No. 55 (Putumayo), c. 200 m, 0°05'N, 75°52'W, August 1980, *Andrade* 33059 (AAU); Río Wai si ayá, 5 km

upstream from outlet in Río Aguarico, 300 m, 0°15'S, 76°21'W, 6 August 1981, *Brandbyge* et al. 33192 (AAU), 10 August 1981, *Brandbyge* et al. 33367 (AAU); Limoncocha on Río Napo, 300 m, 4 March 1974, *Drummond* 7315 (MO); Limoncocha, hunting trail W. of settlement, 243 m, 25 September 1977, *Foster* 3843 (F); Río Jivino, Limoncocha, 13–15 March 1968, *Harling* et al. 7738 (MO); Río Aguarico, E. of Destacamento Zancudo, 310 m, 0°34'S, 75°29'W, 29 August 1979, *Holm-Nielsen* et al. 20178 (AAU); Río Aguarico, SE of Destacamento Largato Cocha, 290 m, 0°10'S, 75°16'W, 30 August 1979, *Holm-Nielsen* et al. 20274 (AAU); union of Río Eno & Río Aguarico, 3–4 km before Secoya village, L. bank of Río Eno, 3 July 1980, *Jaramillo & Coello* 2748 (NY); Río Aguarico, c. 5 km S. of Lago Agrio, 7 November 1973, *Lugo* S. 3240 (MO); Reserva Faunística Cuyabeno, Río Aguarico, Zancudo, behind military camp, 230 m, 0°29'S, 75°32'W, 25 September 1991, *Palacios* et al. 7609 (QCNE); Reserva Cuyabeno, banks of Río Aguarico, Cofán community of Zabalo, 230 m, 0°22'S, 75°45'W, 21 November 1991, *Palacios* et al. 9430 (MO, QCNE); Río Aguarico, town of Dureno, c. 1500 ft, 1 August 1974, *Plowman* et al. 4018 (GH, K).

**PERU. LORETO:** Río Gueppi, tributary of Río Putumayo, N.-most tip of Peru on border with Ecuador, c. 200 m, 15 May 1978, *Gentry* et al. 21886, 21934 (F); Yanamono, Explorama tourist camp between Indiana & mouth of Río Napo, 130 m, 3°28'S, 72°48'W, 18 February 1981, *Gentry* et al. 31383 (MO), c. 120 m, 23 March 1982, *Gentry* et al. 36673 (MO), c. 130 m, 25 June 1982, *Gentry* et al. 37156 (F, MO), 25 July 1982, *Gentry & Alfaro* 37959 (MO), 3°28'S, 72°50'W, 27–28 December 1982, *Gentry & Emmons* 38704 (MO), 28 June 1983, *Gentry & Vásquez* 42285 (MO); Explorama Inn, 1 km S. of Indiana, Río Amazonas, 130 m, 3°30'S, 73°01'W, 17 June 1986, *Gentry* et al. 54613 (MO); Explorama Inn, c. 2 km S. of Indiana on Río Amazonas, 130 m, 3°30'S, 73°02'W, 15 February 1987, *Gentry* et al. 55946 (MO); Explorer's Inn near Indiana, Río Amazonas below Iquitos, 130 m, 3°30'S, 73°03'W, 15 February 1989, *Gentry* et al. 65795 (MO, NY); Explorama Lodge Tourist Camp, Yanamono, far end of Bushmaster trail, halfway between Indiana & mouth of Río Napo, 140 m, 3°28'S, 72°50'W, 5 January 1991, *Gentry* et al. 72167 (MO); Explorama Lodge Tourist Camp, Yanamono, halfway between Indiana & mouth of Río Napo, 130 m, 3°28'S, 72°50'W, 7 January 1991, *Gentry* et al. 72213 (MO); Explorama Lodge, Yanamono, 130 m, 3°28'S, 72°50'W, 11 June 1992, *Gentry* et al. 77492 (MO); environs of Río Santa María, trail one hour E. of Secoya village of Vencedor, 4 hours by outboard from mouth of Río Santa María, c. 1°10'S, 74°44'W, c. 100 m, 12 May 1982, *King* 472 (F); Yanamono, Explorama Tourist Camp on Río Amazonas between Indiana & mouth of Río Napo, c. 80 km NE of Iquitos, c. 100 m, 3°28'S, 72°48'W, 23–27 July 1984, *Knapp* 6606 (BH, K, US, USM); Indiana, Reserva Explorama (Yanamono), 25 km NE of Iquitos, along Río Amazonas, perimeter trail along S. limit, 110 m, 3°30'S, 72°50'W, 27 September 1990, *Pipoly* et al. 12532 (MO); Explorapao camp, inventario MacArthur, near Sucusari, along Río Napo, 100–140 m, 3°20'S, 72°55'W, 3 March 1991, *Pipoly* et al. 14178 (MO); Río Nanay, Chirira, c. 100 m, 21 February 1969, *Plowman* 2548 (GH); Río Ampiyacu, Pebas & vicinity, c. 3°10'S, 71°49'W, 1 April 1977, *Plowman* et al. 6539 (GH); Indiana, Yanamono, Explorama Lodge, 106 m, 3°30'S, 72°50'W, 25 June 1984, *Vásquez* et al. 5120 (MO), 16 May 1989, *Vásquez* et al. 12154 (MO), 29 June 1991, *Vásquez & Jaramillo* 16925 (MO); Explorapao Camp, Río Sucusari, 140 m, 3°15'S, 72°54'W, 25 July 1991, *Vásquez & Grández* 17457 (MO); lower Río Nanay, between Río Nanay & Río Napo, 6 June 1929, *Williams* 709 (F); Pebas on the Amazon River, 24 July 1929, *Williams* 1679 (F).

*Solanum monarchostemon* is sympatric with *S. thelopodium* over nearly its entire range, but does occur higher in the Andean foothills than the latter species. Label data indicate that where they occur together, *S. monarchostemon* occurs in upland, non-inundated forest, while *S. thelopodium* occurs in flooded forests (see above). I have chosen to recognize *S. monarchostemon* at the specific level due to the apparently complete distinguishability of the two sets of plants. Even where *S. thelopodium* and *S. monarchostemon* grow together in the same locality (Yanamono, Peru; Yasuní, Ecuador), no intermediate pubescence types seem to occur. I have seen no mixed collections of the two taxa, again indicative of their apparent distinctness to field collectors. More detailed demographic and populational studies of both taxa in areas where they co-occur may shed light on these differences.

3. *Solanum thelopodium* Sendtn. in Mart., *Fl. Brasiliensis* 10: 46 (1846). Type: Brazil, Amazonas, 'in sylvis ad lacum Teffé, prope Rio Catual, prov. Rio Negro', November, *Martius* 2903 (M!-lectotype, designated here [F neg. 6545-F, G, GH, NY, US]).

Fig. 10

Wand-like shrubs, 0.5–1(–2) m, usually single-stemmed; stems glabrous, drying dark; bark brown. Leaves 11–30(–45) × 4.1–16 cm, elliptic to obovate, usually very thin and membranous, with 12–13 pairs of primary veins, glabrous on both surfaces or with a few scattered papillae along the veins beneath; apex abruptly acuminate; base attenuate; petiole (0.6)–1–2.5 cm. Inflorescences 2–3 times branched from a single point, glabrous or papillate with short trichomes less than 0.5 mm long, the trichomes at most 3-celled and never glandular, the peduncle 2.7–5 cm, the branches 0.5–4 cm, each branch with a single flower open at a time, but with up to 50 scars on each branch. Buds elliptic when young, later markedly pointed and somewhat curved. Pedicels 5–6 mm, glabrous, nodding. Flowers with the calyx tube conical to somewhat flattened, 1–1.5(–2) mm, the lobes deltate to apiculate-deltate to somewhat quadrate, 0.5–1 mm, glabrous or minutely papillose, the apicula with minute trichomes in a tuft at the tip; corolla usually purplish or pink, occasionally white or greenish, 1.5–2 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, 8–9 mm, narrowly triangular with cucullate and papillate tips; filament tube minute, c. 0–0.5 mm; long anther 5–7 × 1–2 mm, the filaments 2–2.5 mm; middle anther pair 3.5–4.5 × c. 1–1.5 mm, the filaments 0.5–1 mm; small anther pair 2.5–4 × c. 1–1.5 mm, the filaments 1–1.5 mm; ovary conical, glabrous; style 8–9 mm, glabrous, gradually widening towards the stigma, the stigma flattened-capitate. Fruit globose, 1–1.5 cm in diameter, green with darker stripes and mottlings, smooth, the pericarp thin and brittle when dry; fruiting pedicel 1.0–1.3 cm, erect. Seeds (5)–10–20 per fruit, 3–4 mm long, pale tan or reddish, flattened to ovate-reniform, the testa cells elongate, sinuate in outline, with markedly and regularly striate outer cell walls.

COMMON NAMES AND USES. Peru, Loreto, 'ocuerilla' (*Ayala* 3112); 'sacha congompe' (*Martin* et al. 1617 – decoction of fresh leaves applied to skin for itching); Brazil, Rondonia, 'capança' (*Prance* et al. 8715).

DISTRIBUTION. Amazonia in Colombia, Ecuador, Peru, Bolivia and Brazil, usually in flooded forest (*igapó* or *tahuampa*), but occasionally in *terra firme* forests, 100–450(–1300) m. Fig. 11.

#### SPECIMENS EXAMINED.

**COLOMBIA.** Amazonas: Boiauassú River, c. 100 m, November 1945, *Schultes* 6787 (F, US); Atacuari River, c. 100 m, 24 October 1946, *Schultes* & Black 8565 (GH, US). Putumayo: Santa Rosa del Río Guamaes, c. 300 m, 2 December 1968, *Plowman* 2100 (GH).

**ECUADOR.** Napo: San Pablo de los Secoyas, 2–5 km W. of the village, 300 m, 0°15'S, 77°21'W, 5 August 1980, *Brandbyge* et al. 32489 (AAU); Río Wai si ayá, 1 km upstream from outlet in Río Aguarico, 300 m, 0°15'S, 76°21'W, 6 August 1981, *Brandbyge* et al. 33209 (AAU); Cantón Archidona, Hollin-Loreto road, between Avila & Loreto, 450 m, 0°43'S, 77°19'W, 24 November 1989, *Cerón* 7767 (MO, QCNE); Cantón La Joya de los Sachas, Pompeya, carretera MAXUS km 3.9–5.2, 250 m, 0°25'S, 76°37'W, 14–15 December 1992, *Gudíño* et al. 2181 (QCNE); Comuna San Isla, Río Napo, c. 3 km E. of Añangu, along Río Garza Cocha, 260 m, 0°29'S, 76°21'W, 8–9 July 1983, *Lawesson* et al. 39821 (AAU); Santa Rosa at Río Napo, 28 April 1972, *Lugo* S. 1999 (MO); Río Bueno, tributary of Río Suno, 4–5 km N. of Santa Rosa, 7 May 1972, *Lugo* S. 2168 (MO); Coca (Puerto Francisco de Orellana), 17 January 1973, *Lugo* S. 2812 (MO); Las Sachas, Coca (Puerto Francisco de Orellana)-Lago Agrio road, 30–40 km E. of Coca, 13 February 1973, *Lugo* S. 3372 (MO). Sucumbíos: Cantón El Chaco, Río Granadillo, INECEL camp Codo Alto, 1300 m, 0°08'S, 77°28'W, 13–15 September 1990, *Palacios* 5634 (QCNE).

**PERU.** Sin. loc., *Matthews* s.n. (K). Huánuco: Finca Panguana, 1 hr walk from Llullapichis on Río Pachitea, on Río Llullapichis, 25 January–15 February 1975, *Dressler* 4934 (MO); Prov. Leoncio Prado, Tingo Maria, Jardín Botánico, Avenida Pimental 358, 670 m, 7 December 1981, *Plowman* & *Ramírez* R. 11192 (F, MO); Prov. Pachitea, Bosque Nacional Iparia, along Río Pachitea near Miel de Abeja camp, 1 km above Tournevista & c. 2 km above confluence with Río Ucayali, 300–400 m, 28 February 1967, *Schunke* V. 1694 (F), 10 October 1967, *Schunke* V. 2201 (F), 16 October 1967, *Schunke* V. 2231 (F). Loreto: Río Afayacu, 10 hrs downriver from Iquitos, 14 December 1980, *Ayala* et al. 2926 (MO, NY × 2); 28 de julio-Río Itaya, 100 m, 25 February 1981, *Ayala* 3112 (F, MO, NY); Padre Isla, in front of Iquitos, 120 m, 27 February 1978, *Díaz* & *Jaramillo* 3 (MO); old Punchana-Nanay road, 5 km N. of Iquitos, 120 m, 27 October 1964, *Dodson* 2863 (MO); Río Amazonas, 2 hrs upriver from Iquitos by 40 h.p. launch, 14 July 1967, *Martin* et al. 1617 (US); vicinity of Iquitos, 1977, *Revilla* 2622 (MO); Sanagal, R. bank of Río Itaya, 1 hr from Iquitos in motorboat, near Yanayaco, 120 m, 4°10'S, 73°20'W, 9 August 1980, *Vásquez* et al. 409 (MO, NY); Prov. Requena, Cocha Apucate, Río Ucayali near Pto. Peru, c. 170 m, 5°15'S, 74°10'W, 5 December 1980, *Vásquez* & *Jaramillo* 904 (MO); Prov. Alto Amazonas, Andoas, L. bank of Río Pastaza, Campamento OXI, c. 210 m, 2°55'S, 76°25'W, 6 June 1981, *Vásquez* & *Jaramillo* 1982 (MO); Padre Isla, Cocha Pastor, 116 m, 3°45'S, 73°10'W, 29 October 1981, *Vásquez* 2685 (MO); Prov. Maynas, Alpahuayo, Estación IIAP, 14 November 1984, *Vásquez* et al. 5695 (MO, NY); Iquito, Caserío Nuevo Jerusalen, Isla Iquitos, 106 m, 3°45'S, 73°15'W, 12 January 1989, *Vásquez* & *Jaramillo* 11516 (MO); Iquitos, Alpahuayo, experiment station of the Instituto de Investigaciones de la Amazonía Peruana (IIAP), 150–180 m, 4°10'S, 73°30'W, 20 January 1991, *Vásquez* 15889 (MO); Las Amazonas, Explornapo camp, Sucusari, cocha Shimigay, 140 m, 3°15'S, 72°54'W, 26 June 1991, *Vásquez* et al. 16859 (MO); along Río Itaya, 14 May 1929, *Williams* 248 (F); Caballo-Cocha on Amazon River, 9 August 1929, *Williams* 2281, 2312 (F); La Victoria on Amazon River, 23 August 1929, *Williams* 2744 (F), 5 September 1929, *Williams* 3110 (F). Madre de Dios: Prov. Tambopata, c. 30 air km or 70–80 river km SSW of Puerto Maldonado at effluence of Río La Torre (Río D'Orbigny)/Río Tambopata, SE bank, Tambopata nature reserve, c. 260 m, 12°49'S, 69°17'W, 3 May 1980, *Barbour* 5117 (MO); Tambopata Reserved Zone, 5.1 km down main trail for Explorer's Inn, near Laguna Cocococha, 12°50'S, 69°17'W, 6 March 1988, *Bell* & *Wiser* 88–10 (US); Tambopata Reserved Zone, near Laguna Chica, 12°50'S, 69°17'W, 15 March 1988, *Bell* et al. 88–192 (US); Río Alto Madre de Dios, near chacra of Sr. Carpio, halfway between Shintuya & Manuy, 10–11 August, 1974, *Foster* et al. 3213 (F); prov. Manu, Río Palotoa (Río Pantiacolla of maps), tributary of Río Alto Madre de Dios NW of Shintuya, 500 m, 26–28 August 1978, *Foster* & *Terborgh* 6709 (F); Pakitsa, entrance to Manu park, 360 m, 26 October 1979, *Gentry* et al. 27258 (MO); Prov. Tambopata, Cuzco Amazonico, 15 km ENE of Puerto Maldonado, 200 m, 12°35'S, 69°05'W, 12 December 1989, *Gentry* et al. 68604 (MO); Prov. Manu, Manu Park, Cocha Cashu uplands, 400 m, 11°45'S, 71°00'W, 18 August 1986, *Núñez* 5768 (MO, NY), 13 September 1986, *Núñez* 6120 (MO, NY); Explorer's Inn, near confluence of Río Tambopata & Río La Torre, 39 km SW of Puerto Maldonado, 12°50'S, 69°20'W, 3 October 1985, *Smith* et al. 533 (US); Prov. Tambopata, Cuzco Amazonico Inn, 200 m, 12°29'S, 69°03'W, 20 January 1991, *Timaná* & *Smith* 1294 (MO), 17 November 1991, *Timaná* 3252 (MO), 22 February 1992, *Timaná* 3717 (MO). San Martín: Prov. Mariscal Cáceres, mouth of Río Mishollo, L. bank of Río Huallaga, 5 February 1971, *Schunke* V. 4701 (F); Quebrada Cañuto, near chacra of Lizardo Aliaga, Dtto. Tochache Nuevo, 500 m, 7 May 1979, *Schunke* V. 10930 (MO).

**BOLIVIA.** Sin. loc., *Rusby* 836 (NY). Beni: Prov. Trinidad, vicinity of Puerto Almacén, 50 m, 22 July 1992, *Rueda* 826 (MO); Prov. Ballivian, Estancia Conquistadora, 56 km E. of the Río Maniqui on road to Trinidad, then 4 km N. to forest island, 250 m, 14°47'S, 66°24'W, 8 November 1985, *Solomon* 14615 (MO). La Paz: Rurrenabaque, 1000 ft, 28 March 1921, *Cardenas* 1874 (NY). Pando: Prov. Nicolas Suárez, near Puerto Rico, banks of Río Tahuamanu, 26 January 1983, *Fernández Casas* & *Susanna* 8491 (NY). Santa Cruz: Prov. Ichilo, along Río Saguayo, Parque Nacional Amboro, c. 5 miles N. of entrance to Río Saguayo into first Andean foothills, 350 m, c. 17°37'S, 63°43'W, 21 January 1988, *Nee* 36031 (NY); Prov. Ichilo, PN Amboro, c. 5 km SE of the Río Surutu, along Río Pitasama, 400 m, 17°40'S, 63°36'W, 31 August 1985, *Solomon* 14190 (MO).

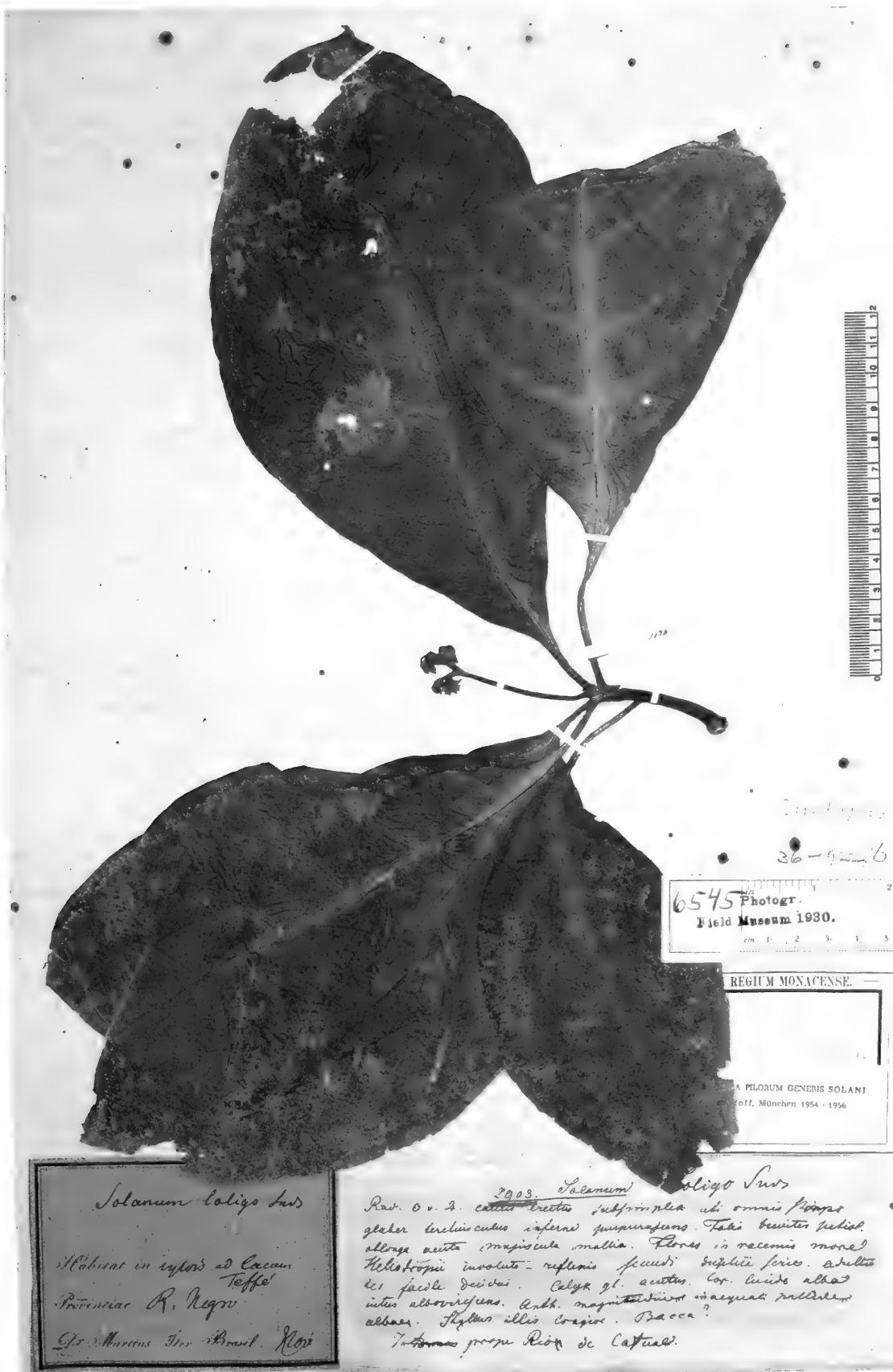
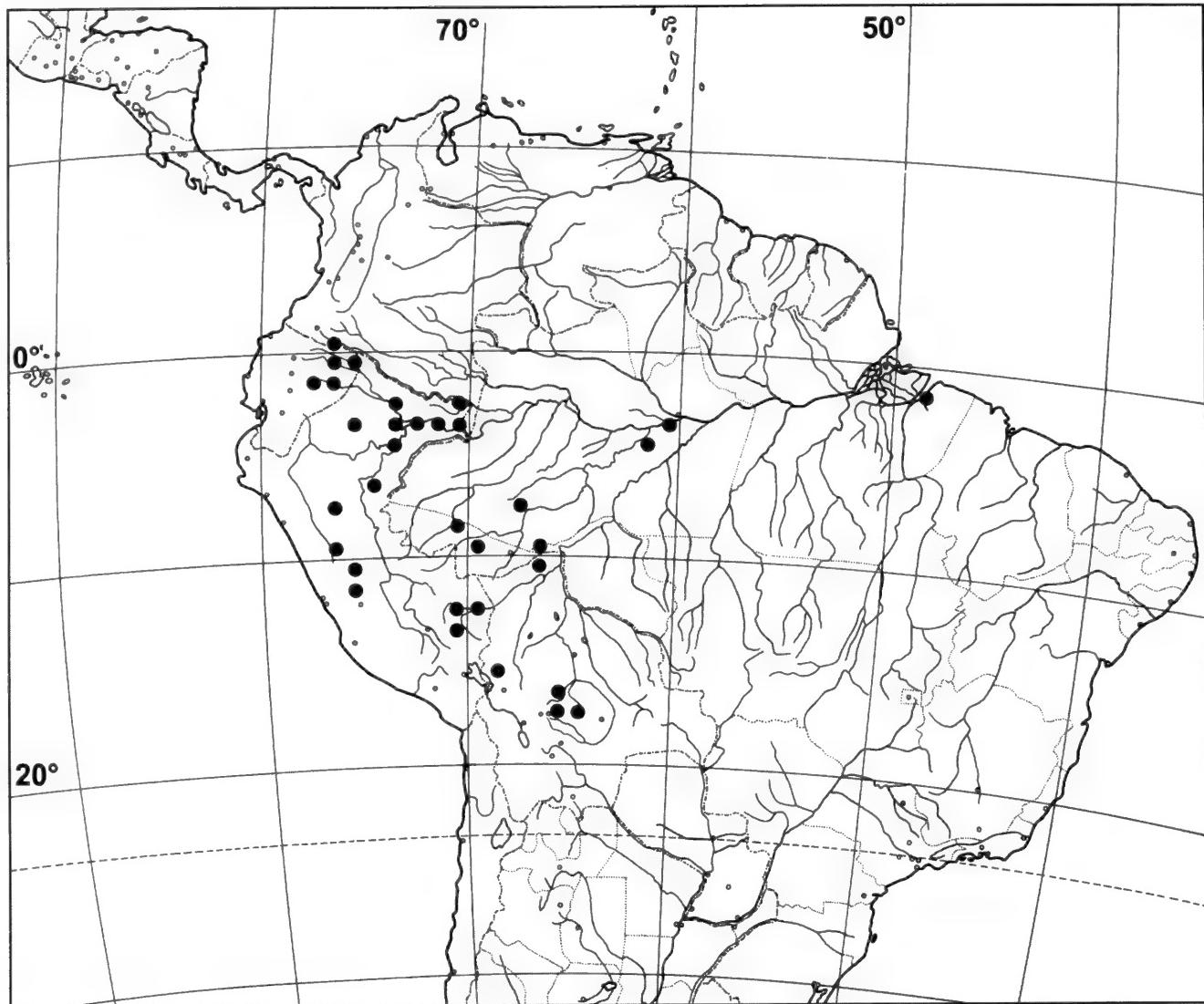


Fig. 10 Lectotype of *Solanum thelopodium* (Martius 2903, Amazonas, Brazil).



**Fig. 11** Distribution of *Solanum thelopodium*.

**BRAZIL.** Acre: Mun. Tarauacá, vicinity of Tarauacá, 13 September 1968, Prance et al. 7242 (NY), 23 September 1968, Prance et al. 7490 (NY); Mun. Sena Madureira, E. of Rio Iaco, 10 km above Sena Madureira, 4 October 1968, Prance et al. 7823 (NY). Amazonas: near mouth of Rio Embira, tributary of Rio Tarauaca, 7°30'S, 70°15'W, 26 January 1933, Krukoff 4998 (NY); Mun. Manicore, near Bella Vista, 8–11 September 1934, Krukoff 6020 (NY); Pamirí dos Ramos, October 1850, Spruce 1129 (K); Marory, Juruá, September 1900, Ule 5206 (HBG); Rio Juruá, Juruá Miry, July 1901, Ule 5691 (B [destroyed: Fneg. 2814, F, G, GH, NY], HBG). Pará: sin. loc., 1826, Siber s.n. (M [Morton neg. 8750 F, GH, NY, US]). Rondônia: basin of Rio Madeira, E. bank of Rio Madeira between Abuña & Penha Colorado, 20 November 1968, Prance et al. 8715 (NY).

*Solanum thelopodium* tends to grow in flooded forest, rather than on the *terra firme*. It also occurs much lower down on the Rio Amazonas than its partially sympatric relative, *S. monarchostemon*. Flower colour in *S. thelopodium* is usually pinkish, while flowers of *S. monarchostemon* are always greenish white. Label data indicate, however, that *S. thelopodium* does sometimes have greenish flowers. This colour polymorphism is common in the spiny solanums, but less so in the non-spiny part of the genus (see Knapp, 1989 for some exceptions).

The thick woody tap-root of *Solanum thelopodium* (see Fig. 2) may be related to its flooded forest habitat. Plants submerged during the wet season probably die back, resprouting as the water recedes during the dry season and flowering and fruiting in a short space of time.

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